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C. H. C. BRUNTON

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BY

C. H. C. BRUNTON x-ref.

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By C. H. C. BRUNTON

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SYNOPSIS

This paper, the second of a series describing the Viséan brachiopods from near Derrygonelly in county Fermanagh, deals with the Inarticulata, Enteletacea, Strophomenacea, Davidsoniacea and Chonetacea. *Brochocarina* and *Serratocrista* are new Davidsoniacean genera and *Globosochonetes* a new chonetid genus; four new species are described. Additional evidence is presented for the separation of *Leptagonia* from *Leptaena* and the relationship of the Chonetacea to the Productacea is discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

This study follows that of the Productacea (Brunton 1966) as part of a series dealing with the brachiopods etched out with acid from Viséan limestones at the Sillees river near Bunnahone Lough, or on the southern shore of the nearby Carrick Lough, about 2 miles N.W. of Derrygonnelly in county Fermanagh, Northern Ireland. All the material is from these localities unless otherwise stated in the text, and is of a Low D zone age. A locality map was given in the previous part (Brunton 1966; 178, fig. 2).

I take pleasure in thanking Professor A. Williams for his help and encouragement while engaged upon much of the work in his department during the tenure of a D.S.I.R. studentship. I am grateful to Dr. H. M. Muir-Wood, late of the British Museum (Natural History); Dr. I. Rolfe, Hunterian Museum, Glasgow; the late Professor R. G. S. Hudson, Trinity College, Dublin; Dr. G. A. Cooper, Smithsonian Institution, Washington; Dr. K. E. Caster, University of Cincinnati; Mr. J. M. Edmonds, University Museum, Oxford and Mr. M. Mitchell, Institute of Geological Sciences, London for the loan of specimens in their care and for advice. Some of the photographs were taken by members of the Photographic Department of the British Museum (Natural History); to them and many other helpers I extend my thanks.

I am grateful for having had my attention drawn to the fact that in my previous publication upon the Productacea (1966) I did not make clear from which locality new taxa were collected. The information is given below:

Dasyalosia panicula Brunton: Carrick Lough.
D. lamnula Brunton: Bunnahone.
Krotovia lamellosa Brunton: Bunnahone.
Eomarginifera (*Eomarginiferina*) *trispina* Brunton: Bunnahone.

II. SYSTEMATIC DESCRIPTIONS

Unless otherwise stated the majority of the specimens here described were collected from the Sillees River locality (Irish Grid Reference 2105 : 3550): other specimens are from the Carrick Lough locality (Irish Grid Reference 2092 : 3538). The fauna from these localities (separated by a distance of 1 mile) are considered to be of the same age (low D Zone).

All specimens prefixed by B or BB are in the collection of the British Museum (Natural History). The depository of other specimens is given in the text.

Class *INARTICULATA*

Suborder CRANIIDINA Waagen 1885

Superfamily **CRANIACEA** Menke 1828

Family **CRANIIDAE** Menke 1828

Genus ***CRANIA*** Retzius 1781

Type species. *Anomia craniolaris* Linné, by subsequent designation of Schmidt (1818 : 71).

Williams (1943 : 70) erected the subgenus *Lissocrania* for " Cranias with dorsal valves devoid of radial costae or spines. Ornamentation, if any, consists of concentric growth lines or of fine radiating striae or both." The type species, *Crania dodgei* Rowley is poorly known and its interior was not described by Rowley (1908), Weller (1914) or Williams (1943). The type species of *Crania* s.s., from the Cretaceous, and the modern *C. anomala* (Müller) are devoid of radial ribbing and may have slightly larger dorsal posterior adductor scars than anterior scars. Thus, with our present knowledge, the retention of *Lissocrania* is unjustified, and in the recently published Brachiopoda Treatise (1965) it is tentatively placed in synonymy with *Crania*.

Other non-ribbed craniid genera are *Petrocrania* Raymond 1911 (= *Craniella* Oehlert 1888) and the poorly known genus *Philhedrella* Kozlowski 1929, originally erected as a subgenus of *Philedra*. Distinction between these two genera may lie in the presence of well defined dorsal mantle canal traces in *Petrocrania* and in its dorsal posterior adductor scars being larger than the anterior scars, apparently unlike *Philhedrella*. In his revision of craniids von Huene (1899) included *C. quadrata* (M'Coy) and *C. kirkbyi* Davidson in *Craniella* (now *Petrocrania*), but as this group is not known to possess sigmoidal mantle canal traces in the dorsal valve they should probably be removed from *Petrocrania*. Conceivably they could be assigned to *Philhedrella* or *Crania*. Species at present within *Philhedrella* range from the Ordovician to Upper Silurian, while *Crania* species are described from the Carboniferous times up to the Recent. As the former genus is inadequately known *Crania* is perhaps the more appropriate genus within which to place *C. quadrata*, the species to which the smooth-shelled Fermanagh craniids are assigned.

There are marked differences in the morphology of Carboniferous and Cretaceous *Crania*. The Mesozoic forms are thick shelled with deeply impressed muscle scars, particularly those of the pedicle valve which are cavernous in form, and a limbus is common. Palaeozoic shells are thin and the muscle scars are commonly raised areas in both valves; the brachial valve is without the internal radial ridges seen between the muscle scars of the Mesozoic forms. Such differences may result from a greater ability of Mesozoic shells to deposit skeletal material and it may prove more realistic to distinguish the Palaeozoic species as a group. A clear understanding of *Philhedrella* may reveal that this genus would be suitable for some non-ribbed Palaeozoic species presently assigned to *Crania*.

Crania quadrata (M'Coy)

(Pl. 1, figs. 1–9)

1844 *Orbicula quadrata* M'Coy: 104, pl. 20, fig. 1.
1861 *Crania quadrata* (M'Coy) Davidson: 194, (1863) pl. 48, figs. 1–13.
1899 *Craniella quadrata* (M'Coy) Huene: 148.

Description. Outline irregular, rounded to subquadrate when undeformed, with gently folded margin, posteriorly flattened to gently sulcate; ventral valve entirely fixed; dorsal valve subconical with beak directed posteriorly and closer to posterior margin; ornamentation of concentric growth lines and scattered short spine-like protuberances, valve margins may be slightly thickened; dorsal anterior adductor scars close to apex, separated by distance equal to width of scar and from less distinct, widely spaced posterior scars situated close to valve margin; slight radial ridge from beak to valve edge between the muscle scars; shell substance punctate.

MEASUREMENTS (in mm.):

	length	width
Incomplete brachial valve (BB.55599)	*c.* 16·5	*c.* 20·0
Complete brachial valve (BB.55600)	7·5	8·6
Complete brachial valve (BB.55601)	3·7	3·9
Complete brachial valve (BB.55602)	2·2	2·3
Complete brachial valve (BB.55603)	2·1	2·4
Incomplete brachial valve (BB.55616)	2·1	1·2

DISCUSSION. The fauna from Fermanagh includes a wide range of sizes, from about 1·0 mm. to an incomplete brachial valve about 20·0 mm. wide. Pedicle valves are absent from the collections. Among the juvenile valves are some small shells of up to 5 mm. long which are almost as high as long and which have well defined narrow posterior trigonal areas. Together with these highly conical valves are more typically proportioned specimens looking more like the larger specimens. It may be that different habitats induced differing juvenile forms or that we have in the collection a different species, only represented by these small shells. An example of these conical forms is figured (Pl. 1, figs. 6, 7). Normally the larger valves are about one-half as high as long.

Valve outline is variable, depending upon the shell's site of attachment and probably upon its degree of crowding, but one well formed specimen, with a high degree of bilateral symmetry may be taken as being typical of undeformed specimens (Pl. 1, figs. 4, 5). The posterior trigonal area is differentiated by a pair of shallow sulci extending from the beak to the valve margin. Anteriorly the margin is slightly bilobed as a result of a third antero-median shallow groove. These features, together with the more posteriorly placed beak, give the valves a distinct orientation. Although appearing smooth externally, save for a few growth-lines, these valves are also ornamented by sparcely scattered more or less concentrically arranged spine-like protuberances. The possibility that these structures are an artifact of the silicification process has been recognized, but rejected on account of their regular development upon the specimens available. Rarely these " spines " can be seen to project at a high angle from the surface, but only for about 0·1 mm., and they are spaced about 0·4 mm. apart. This is considerably more widely scattered than are the " spines " of *Acanthocrania*.

Internally the anterior muscle scars are situated towards the top of the trigonal posterior region, on the slight infolds of the valve, and extend for nearly one-half of the distance towards the margin. The smaller, more rounded posterior scars are not radially aligned with the anterior scars and are only slightly more widely spaced. Dividing the trigonal area is a slight median thickening which is most clearly developed near the somewhat thickened valve margin.

In 1858 Davidson erected the species *Crania kirkbyi*, from the Permian of N.E. England, which he described as being " . . . sub-quadrate, with rounded angles, and is sometimes a little indented at its anterior margin ". Davidson continued by saying that the external surface was closely covered by a multitude of minute, short, hollow, spinose tubercles, which produce a granulated aspect." (1858 : 49). The interior was poorly described. In 1863 Davidson added a note upon the species saying that he thought the granulation was unnatural and that his species may be the same as *C. quadrata* (M'Coy) from the Carboniferous. He figured the two species on plate 54 (1863) and the two appear identical If Davidson's first impressions regarding the granulated looking surface of *C. kirkbyi* were correct it would seem even more likely that the two are conspecific.

Genus ***ACANTHOCRANIA*** Williams 1943

TYPE SPECIES. *Crania spiculata* Rowley (1908), by original designation of Williams (1943 : 71).

Acanthocrania cf. ***laevis*** (Keyes)

(Pl. 1, figs. 10–14)

1894 *Crania laevis* Keyes: 40.
1914 *Crania laevis* Keyes; Weller: 47, pl. 1, fig. 33.

DESCRIPTION. Outline transversely elliptical with flattened posterior margin; ventral valve unknown; dorsal valve deep, lateral profile asymmetric, anteriorly evenly convex, posteriorly steep to concave; beak posteriorly directed and may be below valve apex; ornamentation of sporadic sublamellose growth-lines and closely spaced radially directed spines at low angle to valve surface, arranged more or less concentrically and quincuncially; adductor scars divided, anterior pair just posterior of valve apex, near beak, similarly sized posterior scars close to valve margin and widely separated; shell substance punctate.

MEASUREMENTS (in mm.)

	length	width
Complete brachial valve (BB.55604)	4·6	5·7

DISCUSSION. Wright (1963 : 249) discusses the genus mentioning its range from the Ordovician to the Carboniferous. The first record of the genus from the British Isles is that of Wright for Ashgillian specimens from the Portrane Limestone of Co. Dublin. The type species is a North American Visean form and this Fermanagh record is the first from the upper Palaeozoic of the British Isles.

The specific description of *A. laevis* given by Keyes is inadequate and the species not illustrated. However, Weller (1914) gave a full description, with a figure, of the specimen from " . . . the Burlington Limestone . . . used by Keyes ", and from this it is clear that it is closely comparable to the Fermanagh material. The specific name given by Keyes (1894) is inapt but possibly results from the lectotype being silicified and the papillose surface being thought to result from this process. Keyes noted that the surface was " marked by concentric lines of growth ", but it was Weller who described the papillose or spinose nature of the surface. This external ornamentation is well preserved on the few valves available from Fermanagh and near the margins, where the " spines " are longest, they are up to 0·4 mm. long. These papillae or spines may be morphologically associated with the shell punctuation, which is only clearly visible on the internal surfaces of the Fermanagh specimens. The spines arise from the shell in positions corresponding to the internal positions of punctation and both have similar numbers per unit area, although there are commonly rather more spines. This may result from the coalescence of several juvenile punctae into a single larger puncta within younger parts of the shell. This has been described previously in *Crania* (e.g. Joubin, Blockman) and recently refigured by Rowell (in Williams *et al.* 1965, fig. 77).

Weller's description (1914 : 48) of the brachial valve interior of the American material is accurate for the present specimens and the widely spaced posterior adductor scars are slightly larger than the closely and apically placed anterior scars. The posterior scars are less well defined and it is likely that with age they would have grown more prominent and proportionately still larger than the anterior scars. The margins of the valve are not greatly thickened although slight lamellae were developed.

As there is only one complete specimen, together with fragments, it is impossible to present variation studies on this species. Rarely the brachial valve may have grown in a distorted fashion and may show signs of the skeletal material against which it grew.

Genus ***PHILHEDRA*** Koken 1889

TYPE SPECIES. *Philhedra baltica* Koken by original designation of Koken (1889: 465).

Philhedra trigonalis (M'Coy)

(Pl. 1, figs. 15–29)

1844 *Orbiculata trigonalis* M'Coy: 401, pl. 20, fig. 2.
1899 *Philhedra trigonalis* (M'Coy) Huene: 147.

DESCRIPTION. Outline subrounded to longitudinally subelliptical; profiles asymmetrical and variable with beak posterior of mid-length and at apex of valve; margins of brachial valve irregularly shaped through contact with substrate; growth-lines distinct and commonly interrupting radial ribs which extend from near apex to valve margins, ribs increase in width and added by branching and rare intercalation; brachial valve interior with anterior adductor scars slightly raised, oval, closely placed near beak and divergent towards less distinct ovoid posterior scars which extend close to valve margin; pedicle valve thin and poorly known, with growth-lines and distorted to conform to object of attachment; shell substance punctate.

MEASUREMENTS (in mm.)

	length	width
Complete brachial valve (BB.55608)	11·0	8·4
Incomplete brachial valve (BB.55609)	11·4	c. 7·5
Complete shell attached to rugosochonetid (BB.55607)	8·5	7·5
Complete brachial valve (BB.55610)	8·0	6·7
Distorted brachial valve (BB.55611)	6·9	7·4
Incomplete shell (BB.55612)	5·7	5·6
Complete brachial valve ((BB.55613)	4·0	4·2
Complete brachial valve (BB.55614)	2·7	2·5

DISCUSSION. The Fermanagh sample is varied in size (having a range of from 2·0 mm. to 12·0 mm. long) and outline. The beak is asymmetrically placed and the height of the shells differs from just under one-half to less than one-quarter of the shell length. Ventral valves are rarely preserved and their interiors have not been observed. However, it is clear that these valves were much effected by the substrate; they commonly show growth-lines and are punctate.

The dorsal valve is rounded to subelliptical in outline with little or no posterior flattening, as is common in *Acanthocrania* and *Philhedrella*. The posterior slope is less steep than in these genera although the beak is posterior of mid-length. The larger shells are more elongate than the smaller ones and in profile they retain their height for a short distance before dropping to the anterior margin (Pl. 1, fig. 17). The costae arose within about 1 mm. of the beak and costellae were added by unequal branching or intercalation. The rib crests are somewhat serrated and commonly interrupted by the growth-lines; their width increases slightly towards the valve margins. Some shells became distorted from growth against foreign objects, such as fenestellid colonies, (Pl. 1, fig. 25) and the substrate upon which the shells grew had a marked effect upon the shape of the commissure.

Apart from the adductor scars and punctae the brachial valve interior is devoid of structures. In the present silicified material the punctae are most clearly developed and largest close to the valve margins. One valve has a tent-like ridge anterior of the beak and oblique to the mid-line (Pl. 1, fig. 29). The antero-lateral end of this ridge appears to be broken and there is nothing to suggest that there was another ridge on the opposite side of the shell or that damage to the shell resulted in its formation.

The distinction between *Crania* and *Philhedra* rests principally upon the relative sizes of the muscle scars in the dorsal valve and external ornamentation; *Philhedra* being distinguished as having larger anterior scars than posterior scars and better defined costellate ribbing.

Class *ARTICULATA*

Order ORTHIDA Schuchert & Cooper 1932

Superfamily **ENTELETACEA** Waagen 1884

Family **ENTELETIDAE** Waagen 1884

Subfamily **SCHIZOPHORIINAE** Schuchert & Le Vene 1929

Genus ***SCHIZOPHORIA*** King 1850

TYPE SPECIES. *Anomites resupinatus* Martin 1809, by original designation of King (1850 : 106).

George & Ponsford (1938 : 228) selected a neotype for *S. resupinata* (Martin) and this specimen (BM(NH) BB.2420) was later figured by Bond (1942, pl. 21). The specimen is large; 55·5 mm. long, 72 mm. wide and 32·5 mm. thick, and as Bond said " would approach Demanet's variety *gigantea* " (Pl. 2, figs. 1–3). The Fermanagh shells range in length from 1 mm. to 13·5 mm. and never display the resupination of the pedicle valve commonly seen in large specimens, such as the neotype.

In his study of Carboniferous *Schizophoria* Bond (1942, for 1941) divided the British and Belgium species into those with coarse ornamentation, i.e. with 3 or 4 ribs per mm. about 10 mm. from the umbo, and those species with fine ribbing, i.e. 6–9 ribs per mm., 10 mm. from the umbo. Into the former group he placed *S. resupinata* and its varieties *gigantea* Demanet, *dorsosinuata* Demanet, *lata* Demanet, *pinguis* Demanet, *rotundata* Demanet, and *elboltonensis* George & Ponsford, (which are further united by having dental plates at about 70° from one another) together with the species *S. nuda* George & Ponsford, *S. hudsoni* George and *S. connivens* (Phillips). The type specimen of Phillips' species is lost and his figure (1836, pl. 11, fig. 2) is inconclusive. However, Bond selected a neotype from among specimens in the Gilbertson Collection in the British Museum (Nat. Hist.) (B.387, re-registered as BB.54902) which is distinguished from *S. resupinata* by its more globose profile, near sulciplicate anterior commissure, short hinge line, narrowly divergent dental plates (30°) and small size (16 mm. long). However, Bond admits that only one specimen with such a commissure was seen in his study and that its shape variants grade into some of the more rounded and globular variants of *S. resupinata*. The dental plates are said to be a valid distinction. This being so the Fermanagh shells can not be attributed to *S. connivens* as their dental plates diverge at about 70°, like *S. resupinata* s.s.

George & Ponsford (1938) spoke of *S. dorsosinuata* Demanet as a distinct species and illustrated sections of three specimens that they attributed to Demanet's variety. Two of these illustrations (1938, figs. 11, 14) are of interest in that the brachiophore bases are at an angle to the brachiophores, as are those of the Fermanagh shells. Serial sectioning has confirmed this feature in a topotype specimen of Demanet's var. *dorsosinuata* from Tournai, Belgium (kindly presented by Dr. P. Sartenaer) and has led me to assign the Fermanagh specimens to what I consider the subspecies *S. resupinata dorsosinuata* Demanet. The brachial valve of the neotype is sulcate for approximately the first 50 mm. of its length. This dorsal sulcation is not a common feature but when present most probably produced a unisulcate anterior commissure, similar to that of the present material, before the onset of resupination of their pedicle valves.

Schizophoria resupinata (Martin) ***dorsosinuata*** Demanet

(Pl. 2, figs. 7–37; Text-figs. 1–4)

1861 *Orthis resupinata* (Martin) Davidson (pars.): 130, pl. 30, fig. 1, *non* figs. 2–5.
1934 *Schizophoria resupinata* var. *dorsosinuata* Demanet: 53, pl. 3, fig. 14, 15.
1938 *Schizophoria* cf. *dorsosinuata* Demanet; George & Pensford, figs 11, 14.
1942 *Schizophoria resupinata* var. *dorsosinuata* Demanet; Bond: 289.

DIAGNOSIS. Small, biconvex dorsally sulcate *Schizophoria* with unisulcate anterior commissure; brachiophores subparallel but brachiophore bases diverging to valve floor.

DESCRIPTION. Outline rounded subrectangular, length about four-fifths maximum width, hinge-line straight, about one-half width, cardinal extremities rounded, anterior margin gently rounded to emarginate and commissure slightly unisulcate; profile biconvex, depth about one-half length, increasing with age; gentle dorsal sulcation; radial ornament of low rounded and delicate ribs, about 14 in 2·5 mm. at 5 mm. antero-medianly from dorsal umbo, about 10 costae and first order costellae commonly remaining prominent; branching by intercalation and rib apertures well developed; concentric ornament sporadic but distinct; ventral interarea concave, apsacline, delthyrium triangular, open; dorsal interarea about one-half length of ventral interarea, curved anacline, with open notothyrium, chilidium obsolete; teeth strong, triangular in outline and diverging at about 45° from mid-line, supported by receding divergent plates fused posteriorly to inner surfaces of umbonal slopes; notch below teeth articulating with apophyses on brachiophores; base of dental plates extending anteriorly as ridges laterally enclosing oval muscle scars about two-fifths valve length; muscle field width about three quarters its length and medianly divided by strong anteriorly widening ridge on antero-lateral faces of which are narrow lanceolate adductor scars; mantle canal traces obscure, but pair of strong *vascula media* extend anteriorly from anterior ends of each diductor scar; cardinal process developed as ridges across floor of notothyrial cavity, between brachiophore bases, with distally expanded and incised myophore, trilobed in adults; brachiophores strong, diverging at about 40° from mid-line, median faces vertically disposed and fulcral plates well developed; brachiophore bases diverging to valve floor, continued anteriorly as indistinct ridges surrounding adductor field but interrupted by traces of three mantle canals; adductor field about four-ninths valve length and about as long as wide, divided medianly and into posterior and anterior scars; marginal follicular embayments may persist posteriorly.

MEASUREMENTS (in mm.)

	length	width
Complete shell (BB.52701)	13·8	16·0
Complete shell (BB.52702)	13·0	—
Pedicle valve (BB.52703)	11·3	14·5
Incomplete brachial valve (BB.52705)	12·5	—
Complete brachial valve (BB.52707)	3·1	3·7
Complete brachial valve (BB.52708)	3·8	4·6
Complete brachial valve (BB.52709)	5·5	6·7
Incomplete brachial valve (BB.52711)	*c.* 16·0	—
Complete pedicle valve (BB.52713)	2·0	2·6
Complete pedicle valve (BB.52714)	7·0	8·5
Incomplete brachial valve (BB.52715)	*c.* 11·5	—
Complete shell (BB.52716)	2·9	3·6
Complete shell (BB.52717)	1·3	1·6

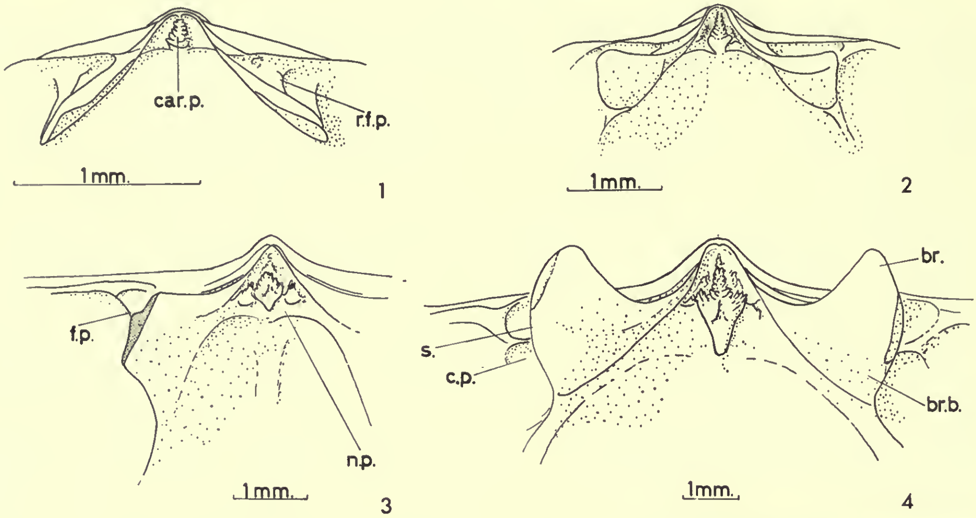
DISCUSSION. The present Fermanagh *Schizophoria* specimens accord most closely with Demanet's variety from the Tournaisian of Belgium. Similar specimens were described by Sanders (1958 : 43) from rocks of Kinderhook age in Mexico under the new name *S. sulcata.* This silicified material shows interiors comparable to those from Fermanagh although the Mexican shells are about 10 mm. longer and relatively thicker. The cardinal process's of both faunas are comparable in having a bifid central lobe and a pair of lateral lobes within the notothyrial cavity (Sanders 1958, pl. 3, fig. 19, cf. Pl. 2, fig. 17). Sanders characterizes his species by " the sulcus on each valve ", (p. 44) but only that on the dorsal valve is clear from his figures.

The external radial ornamentation arose from the initial 10 or 12 costae by the apparent intercalation of costellae, mostly posteriorly. The costae arose within 0·3 mm. of the umbones of each valve. The brachial valve commonly had a median costa for about the first 3 mm. of growth which subsequently was usually diverted to one side of the median sulcus. First order costellae were added at about 0·5 mm. and second order costellae may show at a length of 1·5–2·0 mm. These additions appear as intercalations, but on close study it is usually possible to determine from which parent rib the costella had arisen, and in this way it can be seen that there is a tendency towards median branching across the sulcus and lateral branching on the dorsal flanks. On pedicle valves lateral branching is more common in a manner similar to that illustrated by Williams & Wright (1963 : 23). Biernat (1959 : 61) records 12 ventral and 13 dorsal costae on *S. striatula* from the mid-Devonian of Poland. These arose at a length of about 0·45 mm. and with a further 0·5 mm. of growth both first and second order costellae arose. On young specimens a few mm. long, only the apical tips of the beaks are free of costae and these areas represent the brephic valves and protegulal nodes. On Fermanagh shells the ribs are low and rounded and increase in size only slightly towards the anterior margins so that 2, 6, 8, 3 and 1 specimens have respectively 12, 13, 14, 15 and 16 ribs in 2·5 mm. at a distance of 5 mm. from the dorsal umbo. Along the costae and primary costellae, which commonly remain rather larger than the intervening ribs, rib apertures (" hollow costellae " of Schuchert & Cooper, 1932 : 143) occur 3 or 4 times per 10 mm. length. This frequency appears to be less than illustrated by Davidson (1861, pl. 30, fig. 1d) or Sanders (1958, pl. 3, fig. 22) but is probably the result of their increased occurrence with age and size of the shell. These apertures have been interpreted as small spine bases viz. Davidson (1861 : 130), Dunbar & Condra (1932 : 54 and Cvancara (1958 : 857). Demanet figures what he describes as an external impression of a brachial valve (1934, pl. 3, fig. 13) of *S. resupinata* var. *rotundata* Demanet showing minute needle-like rods of iron oxide extending away from the mould into what must have been shell substance. Demanet (1934 : 52) is undoubtedly correct in interpreting these minute rods as being infillings of the shell punctae. There is no clear evidence yet available indicating the significance of the rib aperatures. If, however, their open nature at the valve margins, prior to secondary shell deposition, indicates a functional origin at the mantle margins, it seems likely that the apertures may have assisted in the sensory apparatus of the shell in a way comparable to the "sensory" spines described by Rudwick (1965 : 610). The development of the ventral interior can be traced readily from valves of less than 2 mm. long, by which stage the bilobate muscle field was well developed (Pl. 2, fig. 32). The teeth were not differentiated from the interarea until the valve was about 6 mm. long, but the dental plates were already strongly formed and fused with the inner surfaces of the valve posteriorly. Only along their anterior margins did the dental plates remain discrete from the valve. The ridges enclosing the lateral margins of the muscle field were developed by this stage, as was the strong median ridge, but differentiation within the muscle field is impossible to distinguish. Indeed, it is commonly impossible to see the narrow adductor scars on the median ridge or the narrow lateral lobes of the diductor scars even on the largest shells available. The ventral adjustor scars are rounded trigonal markings upon the inner surfaces of the dental plates.

The coefficients of correlation for all measured parameters are high (see Tables 1, 3) indicating a regular proportional growth. The increased curvature anteriorly of the brachial valve results in an allometric effect for length relative to width ($p \leqslant 0{\cdot}01$), but is not apparent in the sample for other paired parameters. In his studies of *S. resupinata* s.l. from the Lower Carboniferous reefal limestones of northern England, Parkinson (1954) illustrates a possible allometric change in the growth ratios of plots of thickness against length or width at a shell width of about 20 mm. As has been pointed out by Veevers (1959), allometry cannot be clearly indicated without tests of significance having been applied to differing sectors of the growth axis, and this Parkinson did not do.

The shallow dorsal sulcus became distinguishable in valves about 3 mm. long, but became prominently developed between 5 and 10 mm. from the umbo and persisted to the anterior margin. Internally the dorsal muscle field is discernible in shells about 2 mm. long, as is the small knob-like cardinal process and, rarely, the two median mantle canal traces. When the valve was about 3 mm. long a small ridge started to develop on the postero-lateral surfaces of the brachiophores, within the sockets, which grew anteriorly to form fulcral plates. These were not sufficiently developed to arch the crural pits until the valve was about 5 mm. long. At this stage the brachiophore tips were about 2 mm. apart, and although the median ridge had not yet developed between the adductor scars, they were divided into anterior and posterior scars by a laterally directed pair of mantle canals (Pl. 2, fig. 30).

The growth of the cardinal process took place from the apex of the notothyrial chamber as a longitudinally disposed ridge, to the ventral surface of which were attached the diductor muscles. The ridge was not divided distally into myophore lobes, as is commonly found in adult dalmanellids, and the muscle bases presumably extended along its length and onto its flanks. (Text-fig. 1). Shell thickening at the base of the cardinal process built a notothyrial platform, distinguishable in valves about 6 mm. long. This platform remained sunk below the dorsal interarea and even in adult Fermanagh shells was no more than 1 mm. long. During growth the diductor muscle bases must have spread laterally onto a pair of ridges (Text-figs. 2, 3) which developed from the notothyrial platform with deeply crenulated crests, like that of the median cardinal process itself (Pl. 2, fig. 20). In valves over 10 mm. long a variable degree of fusion occurred between these lateral ridges and the main median myophore so that the antero-ventral face of the cardinal process and notothyrial platform became trilobed with the notothyrium almost filled by the three myophore ridges (Text-fig. 4). Additional shell deposition antero-laterally on the median lobe may have resulted in it having become bifid and in its covering the two



Figs. 1-4. Illustrations of the ontogeny of the cardinalia of *Schizophoria resupinata dorsosinuata* Demanet showing the development of the trilobed cardinal process from the notothyrial platform; *br*, brachiophore; *br.b*, brachiophore base; *car.p*, cardinal process (juvenile primary lobe); *c.p*, crural pit; *f.p*, fulcral plate (in Fig. 3 the brachiophore tip is not drawn so as to reveal the fulcral plate); *n.p*, notothyrial platform; *r.f.p*, rudimentary fulcral plate on juvenile specimen; *s*, socket.

lateral lobes. The adult cardinal process is, therefore, a composite trilobed structure, as reported by Demanet (1934 : 47), built principally of the median primary lobe, but accompanied by secondary lateral lobes added during growth.

In discussing the cardinal process of British Avonian *Schizophoria* George & Ponsford (1938 : 233) illustrate serial sections of several specimens and conclude that, while it is variable in form, the cardinal process commonly consists simply of a median serrated " node ". Section 4c, of *S. nuda* George & Ponsford, would be like that of the Fermanagh specimens if the " accessory processes " flanked the median ridge rather than both being on one side. It is possible that less widely spaced sections would have revealed the secondary lateral lobes and the more ridge-like nature of the cardinal process across the notothyrial floor. A comparison of type material of *S. nuda*, preserved as internal moulds in the British Museum (Natural History) (BB.2407–2411), with brachial valve interiors reasonably assigned to *S. resupinata* s.s. (Pl. 2, figs. 5, 6) shows that the two are probably comparable within the limits of specific variation. Bond retained *S. nuda* principally because of its unusual state of preservation, but this hardly seems a worthy reason for specific distinction.

In her study of Mid-Devonian orthoids from Poland, Biernat (1959 : 57) describes and figures the variation to be seen in the cardinal process of adult *Schizophoria striatula* (Schlotheim). She writes that the cardinal process " may be single or bifid ", although it would seem from her figures (1959, text-fig. 20, and pl. 9, figs. 1, 2) that the cardinal process of her material probably grew in a similar way to that of the Fermanagh specimens, viz. the variation being around a basically trilobed structure. The difference would seem to be one of terminology, for in her discussion of the ontogeny of the cardinal process, Biernat describes how " 2 or 3 elevations appear in the notothyrial cavity on each side of the cardinal process " and continues by

TABLE 1

$\bar{\mathrm{l}}$ mm. (var.) = 6·76 (14·613)
$\bar{\mathrm{w}}$ mm. (var.) = 8·42 (22·280)
r = 0·996
a (var.) = 1·235 (0·00111)

$\bar{\mathrm{l}}$ mm. (var.) = 6·76 (14·613)
$\overline{\mathrm{th}}$ mm. (var.) = 2·01 (1·189)
r = 0·990
a (var.) = 0·285 (0·00015)

$\bar{\mathrm{w}}$ mm. (var.) = 8·42 (22·280)
$\bar{\mathrm{x}}$ mm. (var.) = 4·79 (8·355)
r = 0·987
a (var.) = 0·612 (0·00089)

$\bar{\mathrm{l}}$ mm. (var.) = 6·76 (14·613)
$\overline{\mathrm{dl}}$ mm. (var.) = 2·72 (2·838)
r = 0·992
a (var.) = 0·441 (0·00028)

$\overline{\mathrm{dl}}$ mm. (var.) = 2·72 (2·838)
$\overline{\mathrm{di}}$ mm. (var.) = 1·95 (0·866)
r = 0·974
a (var.) = 0·552 (0·00142)

TABLE 1. Statistics of length (l), maximum width (w), width of hingeline (x), thickness (th), and length (dl) and width (di) of the diductor muscle scars of 13 pedicle valves of *Schizophoria resupinata dorsosinuata* Demanet.

TABLE 2

No. of ribs.	12	13	14	15	16
No. of specimens	2	6	8	3	1

TABLE 2. The number of ribs counted in a width of 2·5 mm., 5 mm. antero-medianly from the umbo of 20 pedicle valves of *Schizophoria resupinate dorsosinuata* Demanet.

TABLE 3

$\bar{l}$ mm. (var.) = 5·14 (7·398)
$\bar{w}$ mm. (var.) = 6·42 (11·899)
r = 0·998

$\log_e \bar{l}$ (var. $\log_e$ l) = 1·514 (0·2469)
$\log_e \bar{w}$ (var. $\log_e$ w) = 1·552 (0·2791)
r_e = 0·997
α (var.) = 1·063 (0·00045)

$\bar{w}$ mm. (var.) = 6·42 (11·899)
$\bar{x}$ mm. (var.) = 3·01 (2·714)
r = 0·998
a (var.) = 0·478 (0·00006)

$\bar{s}$ mm. (var.) = 1·18 (0·206)
$\bar{t}$ mm. (var.) = 1·92 (0·503)
r = 0·963
a (var.) = 1·563 (0·0119)

$\bar{l}$ mm. (var.) = 5·14 (7·398)
$\overline{th}$ mm. (var.) = 1·31 (0·441)
r = 0·926
a (var.) = 0·244 (0·00053)

$\bar{l}$ mm. (var.) = 5·14 (7·398)
$\overline{ad}$ mm. (var.) = 2·31 (1·446)
r = 0·987
a (var.) = 0·442 (0·00034)

$\overline{ad}$ mm. (var.) = 2·31 (1·446)
$\bar{v}$ mm. (var.) = 2·18 (0·773)
r = 0·949
a (var.) = 0·731 (0·00213)

$\bar{l}$ mm. (var.) = 5·14 (7·398)
$\bar{s}$ mm. (var.) = 1·18 (0·206)
r = 0·976
a (var.) = 0·167 (0·00020)

TABLE 3. Statistics of length (l), maximum width (w), thickness (th), width of hinge-line (x), length of adductor scars (ad), width of adductor scars (v), length of the extent of the brachiophores (s) and the width at the brachiophore tips (t) of 17 brachial valves of *Schizophoria resupinata dorsosinuata* Demanet.

saying that the adult anterior aspect may be " multifid " while the lateral elevations became thicker and " together with the cardinal process fill all width of the notothyrial cavity ". It seems, therefore, that she retains the term cardinal process only for the central " single or bifid " ridge within the notothyrial cavity and looks upon the lateral " elevations " as being separate structures. She does not indicate a function other than that of diductor muscle attachment, nor does she differentiate the " cardinal process " from lateral elevations in text-fig. 20 (1959 : 57) and it would seem more reasonable to include all outgrowths of the notothyrial platform as constituents of the cardinal process. The intimacy and degree of fusion between the lateral ridges and the median ridge preclude the possibility that the lateral ridges bore the dorsal adjustor muscles.

The internal surfaces of the valves are variably thickened, specimens from Carrick Lough commonly being thinner than those from Bunnahone. In these thinner shelled specimens traces of the radial mantle canals are more prominent, being marked by low bordering ridges, and are represented externally by slightly accentuated radial ribs. A deepening of these canal traces is usually terminated anteriorly by a rib aperture (Pl. 2, fig. 37) which only retained a broad connection to the outer surface while still close to the valve margin. In some young thin-shelled forms up to 7 or 8 mm. long, the traces of each follicular embayment can be followed back to the muscle field, but more commonly secondary shell obscured these, except over the last 1 mm. towards the valve margin. All these traces probably mark the positions of small mantle canals that led to each setal follicle at the mantle edges.

Accentuated " growth-lines " tend to be more crowded anteriorly, indicating retradations of late growth, and it may be that these specimens were living in conditions marginal to their optimum habitat so never reaching a size more typical for the species.

Family **RHIPIDOMELLIDAE** Schuchert 1913

Genus ***RHIPIDOMELLA*** Oehlert 1890

Type Species. *Terebratula michelini* L'Eveillé, by original designation of Oehlert (1890 : 39).

Rhipidomella michelini (L'Eveillé) 1835

(Pl. 3, figs. 1–25, Text- fig. 5)

Diagnosis. Gently dorsibiconvex *Rhipidomella* with prominent, trifid cardinal process and well developed posteriorly convex chilidial plates; ventral diductor scars subrhombiodal in outline, about three-fifths valve length and without strong postero-laterally enclosing ridges.

Description. Outline subrounded to rounded trigonal, hinge-line about two-fifths maximum width which is anterior of mid-length, length slightly less than width, adult anterior margin only gently curved; profile biconvex with depth slightly less than one-half length; slight median sulcation of brachial valve and antero-median flattening of pedicale valve; multi-costellate with 9 or 10 ribs in 2·5 mm., 5 mm. antero-medianly from dorsal umbo, costellae added by bifurcation; growth-lines sporadic and prominent; ventral interarea concave, apsacline, dethyrium open with apical angle of about 80°; dorsal interarea shorter, orthocline to anacline, notothyrium more or less closed by chilidial plates; teeth strong, diverging antero-dorsally at about 40° from mid-line, dental plates vertically disposed but slightly divergent to valve floor; pedicle callist developed apically, dental plates with anteriorly directed notches to receive postero-ventral apophyses of brachiophores; adductor field small, oval to rectangular and anteriorly raised; diductor scars variably impressed, adult scars lobate to subflabellate, surrounding adductor scars, anteriorly ridged and surrounded by slight thickening from bases of dental plates; valve margins strongly crenulated; cardinal process prominent, distally trifid with median ridge extending beyond lateral ridges, postero-laterally enclosed by chilidial plates from below which strong brachiophores extend at 35° to 40° from mid-line; inner faces of brachiophores curved, and bases recurved to floor of valve to enclose deep sockets; adductor field quadrate to trigonal, extending about one-half valve length and separated by low wide ridge which may accommodate dorsal adjustor muscle scars posteriorly, adductor scars possibly divided with more prominent rounded-quadrate anterior scars.

MEASUREMENTS (in mm.)

	length	width
Complete shell (BB.52718)	10·9	11·7
Pedicle valve (BB.52719)	8·8	—
Complete pedicle valve (BB.52720)	9·2	9·9
Incomplete pedicle valve (BB.52721)	—	*c.* 15·0
Complete brachial valve (BB.52722)	7·6	8·5
Brachial valve (BB.52723)	7·0	7·3
Complete shell (BB.52724)	4·6	5·0
Young pedicle valve (BB.52725)	3·4	3·6
Young brachial valve (BB.52726)	3·4	3·6

DISCUSSION. Unlike many species of *Rhipidomella*, which are dorsibiconvex, the present material is almost equibiconvex. While both valves are approximately equal in depth, the convexity of the pedicle valve is greatest posteriorly, close to the umbo, and that of the brachial valve near to its mid-length. These differences are associated with the anterior flattening of the pedicle valve and the median to antero-median slight sulcation of the brachial valve; features which led to a faintly bilobed body cavity. The form of the valve profile is also associated with the radial ornament. It can be demonstrated that there is a distinct tendency for branching of costae and costellae to occur downslope, i.e. over the medianly sulcate region of the brachial valve branching took place more commonly from the median sides (" internal " of Bancroft (1928 : 60)), whereas on the flanks, branches commonly arose laterally (" externally " Bancroft) (Williams & Wright 1963 : 22). The relationship between the mantle edge and the shell margins of dalmanellids has been discussed by Williams & Wright (1963 : 19), and it seems likely that the radial ornament of such shells is intimately associated with the mantle canal system. The grooves seen at certain growth stages on some of the follicular eminences, the shell protuberances between each setal follicle, can be related to external rib branchings. These grooves soon reached the dimensions of the previously formed follicular embayments and became buried in secondary shell deposits posteriorly, so that it is only rarely possible to see the positions of the branchings internally. However, externally they are commonly clear and probably accurately mark the positions of canal and follicular proliferations.

The follicular eminences and embayments form a prominent marginal crenulation in rhipidomellids. The use of these crenulations for supra-specific taxonomic discrimination raises difficulties. Crenulations vary in detail according to both the age of the brachiopod and their distance from the margin of the shell. Certainly the Fermanagh specimens, believed to be conspecific with the type species of *Rhipidomella*, show variation in the cross-section of their crenulations (Text-fig. 5) at different distances from the margin. It is important, therefore, to define closely any such variation used as taxonomic criteria.

A comparision of a small collection of *R. henryhousensis* Amsden, recently placed in *Dalejina* by Boucot *et al.* (1963 : 337), with the Fermanagh specimens shows that differences in their marginal crenulations exist, but other differences may be noted; the absence of chilidial plates and more equally branching ribs in the American species. These differences are, at the best, merely observations, as the American material at hand appears to be slightly abraded. A more equal rib branching, i.e. one in which the branching approaches dichotomy, in *R. henryhousensis* could explain the more regular grooves on the follicular eminences at the valve margins. This seems to be fairly persistent throughout ontogeny, whilst in the Fermanagh specimens a closely comparable style of branching was usually restricted to the first few mm. of growth.

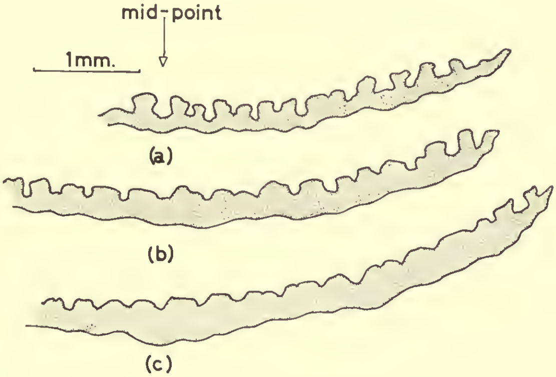


FIG. 5. Three transverse sections parallel to the hinge-line of *Rhipidomella michelini* (L'Eveille) showing the anterior internal marginal crenulations. The mid-point of the shell is indicated on the sections which are 0·4 mm., (a), 0·6 mm.; (b), and 0·8 mm.; (c) from the anterior edge of the shell.

The rib apertures (or hollow ribs) of *Rhipidomella* are well known and have,been assumed to be the bases of spinose extensions of the shell (Davidson 1861 : 133, pl. 30, figs 6, 7). The frequency of these apertures is not constant in *R. michelini*, but is commonly 3 in 5 mm. length of rib. The apertures face anteriorly and away from the valve surface at a low angle, their openings being hooded by the rib posteriorly. Anteriorly the rib is suppressed for a short distance leaving a slight depression. At no time has any sign of spine-like prolongations been seen attached to the valves, either from the Fermanagh fauna or from specimens from Clattering Dykes, possibly figured by Davidson (1861, pl. 30, fig. 6). The openings lead posteriorly along the rib and into the shell substance at a narrow angle. However, only marginally do they open internally on to the floor of one of the follicular embayments. Because of the rapid infilling of these embayments by secondary shell, the openings do not persist over the internal surfaces and, therefore, could not have contained living tissue unless connected by thin strands, such as those joining to the caecae. It is conceivable that the apertures were analogous to the hollow spines of productoids (also commonly marginal) in providing some sort of sensory receptors.

In all known aspects other than the prominence of the muscle scars, in particular the ventral diductor scars, the shells of the Fermanagh fauna agree with the type species *R. michelini* (L'Eveillé), as described by Demanet (1934 : 37, pl. 2). Although the longest valves reach about 12 mm. the muscle scars are all faintly impressed and it seems clear that differential shell deposition alone was responsible for the prominence of the scars found in larger specimens of *R. michelini*.

Campbell (1957 : 51) casts doubt upon the assumption that the dorsal adductor scars were divided into two pairs in the Lower Carboniferous species. Judging from the present material and topotypic material from Belgium (Pl. 3, fig. 5) his doubts seem valid, and no posterior scars have been distinguished with certainty. Demanet (1934 : 39), Dresser (1954 : 22), and Campbell (1957) believe the pedicle callist (Schuchert & Cooper 1932 : 9) to be the seat of the ventral pedicle adjustor muscles. However, it is more likely that it developed because of the anterior retreat of the junction between the pedicle and outer epithelium (Williams 1956 : 255, who termed it the " pedicle collar "). The umbonal cavity, between the dental plates, probably accommodated the base of the pedicle, to which were attached adjustor muscles extending antero-laterally across the cavity floor onto the bases of the dental plates. The dorsal adjustor muscles probably passed between and anterior to the dorsal ends of the diductor muscles and were attached posteriorly between the dorsomedian bases of the brachiophores, close to the base of the cardinal process.

Table 4

$\bar{l}$ mm. (var.) = 4·69 (8·340)
$\bar{w}$ mm. (var.) = 5·01 (8·836)
r = 0·997
a (var.) = 1·029 (0·000213)

$\bar{w}$ mm. (var.) = 5·01 (8·836)
$\overline{b_2}$ mm. (var.) = 1·64 (0·523)
r = 0·941
a (var.) = 0·245 (0·00045)

$\bar{l}$ mm. (var.) = 4·69 (8·340)
$\bar{x}$ mm. (var.) = 2·34 (1·709)
r = 0·995
a (var.) = 0·452 (0·00014)

$\bar{x}$ mm. (var.) = 2·34 (1·709)
$\bar{y}$ mm. (var.) = 2·20 (1·488)
r = 0·992
a (var.) = 0·936 (0·00046)

$\overline{b_1}$ mm. (var.) = 0·74 (0·138)
$\overline{b_2}$ mm. (var.) = 1·64 (0·523)
r = 0·939
a (var.) = 1·947 (0·0298)

Table 4. Statistics of length (l), maximum width (w), length to which the adductor scar extends (x), width of adductor scars (y), and the widths of the brachiophores at their junctions to the interarea (b_1) and at their anterior tips (b_2) in 17 brachial valves of *Rhipidomella michelini* (L'Eveillé).

TABLE 5

Delthyrial angle	65°	70°	75°	80°	85°
No. of specimens	1	3	3	8	2

TABLE 5. The total angle of divergence of the teeth and margins of the delthyrium, in 17 pedicle valves of *Rhipidomella michelini* (L'Eveillé).

TABLE 6

$\bar{l}$ mm. (var.) = 4·39 (6·200)
$\bar{w}$ mm. (var.) = 4·70 (6·859)
r = 0·995
a (var.) = 1·052 (0·00031)

$\bar{l}$ mm. (var.) = 4·39 (6·200)
$\overline{th}$ mm. (var.) = 2·06 (0·915)
r = 0·989
a (var.) = 0·384 (0·00009)

TABLE 6. Statistics of length (l), width (w), and thickness (th) of 20 shells of *Rhipidomella michelini* (L'Eveillé).

TABLE 7

No. of ribs	8	9	10
No. of specimens	4	7	6

TABLE 7. The number of ribs in a width of 2·5 mm., 5 mm. antero-medianly of either umbo on *Rhipidomella michelini* (L' Eveillé).

Order STROPHOMENIDA Öpik 1934

Superfamily **STROPHOMENACEA** King 1846

Family **LEPTAENIDAE** Hall & Clarke 1894

nom transl. Cooper 1956

Subfamily **LEPTAENINAE** Hall & Clarke 1894

Genus ***LEPTAGONIA*** M'Coy 1844

1844 *Leptagonia* M'Coy: 116 (pars).
1846 *Leptaena* King: 28 (pars).
1852 *Leptaena* (*Leptagonia*) M'Coy: 223 (pars).
1861 *Strophomena* Davidson: 119 (pars).
1929 *Leptagonia* Schuchert & LeVene: 74.
1947 *Pseudoleptaena* Miloradovich: 96.
1952 *Leptaenella* Sokolskaja: 35, *non Leptaenella* Fredericks 1917.
1958 *Leptagonia* M'Coy; Cvancara: 859.

DIAGNOSIS. (emended) Biconvex, strongly geniculate and rugose Leptaenidea; ventral and dorsal muscle scars situated upon prominent pseudospondylium and complex muscle platforms respectively.

Description. Outline irregularly quadrate, profile of adult disc biconvex, dorsally directed trail variably developed, commonly affected by opposite folding; rugae regularly and concentrically developed on disc; costae fine, even, rarely branching dichotomously; ventral interarea apsacline, delthyrium wide, covered apically by pseudodeltidium in various stages of resorption, foramen supra-apical, commonly sealed in adult shells; dorsal interarea short anacline, chilidium large; teeth strong, widely divergent, crenulated; dental lamellae continuous with subcircular pseudospondylium, elevated anteriorly; lanceolate adductor scars on broad median ridge; antero-lateral areas of ventral disc rarely raised as low mounds; cardinal process lobes strongly projecting from beneath chilidium with posteriorly directed myophores and strongly curved bases defining subcircular hollow; dorsal adductor field borne on complex platform with elevated subquadrate posterior scars, highly arched in young valves, flanking raised triangular to rectangular anterior scars separated posteriorly by low ridge of secondary shell and anteriorly by deep groove from which median septum extends anteriorly; adult disc enclosed anteriorly by secondary ridge; mantle canal system pinnate to lemniscate; shell substance pseudopunctate.

Type Species. *Producta analoga* Phillips by subsequent designation of Schuchert & LeVene (1929 : 74).

Discussion. The genus *Leptagonia* was originally established by M'Coy in 1844, and was later defined by him as including shells with " both valves abruptly bent at right angles towards the entering " (brachial) " valve and the rostral portion concentrically wrinkled " (1852 : 233). This was done in the belief that *Leptaena* Dalman was typified by *Leptaena transversalis* Dalman (now *Plectodonta transversalis*, and thereby restricted to plectambonitacean-like shells).

Six species were described by M'Coy and assigned to *Leptagonia*, the first being *Producta analoga* Phillips, a poorly defined species from the Lower Carboniferous of Bolland, Yorkshire, and Redesdale, Northumberland, but at that time believed to be closely related to *Leptaena depressa* J. de C. Sowerby and *L. rugosa* Dalman from the Upper Silurian and Upper Ordovician respectively, and also to *Productus plicatilis* J. de C. Sowerby (now type species of *Plicatifera* Chao. from the Carboniferous). In 1855 he included *Leptaena distorta* J. de C. Sowerby within *Leptagonia*, a species also from the Lower Carboniferous.

Davidson (1861 : 119–122) concluded that *L. depressa*, *L. analoga* and *L. distorta* were synonymous and did not merit more than varietal rank of *Strophomena rhomboidalis* (Wahlemberg).

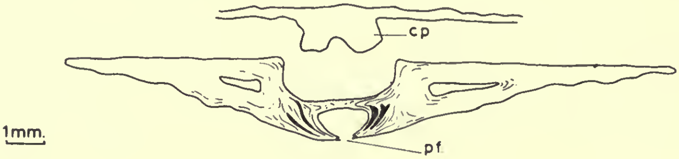
In describing *Leptaena* as a species of *Strophomena*, Davidson was exercising the conservatism that pervaded his approach to brachiopod systematics, because King (1846) had already named a rugate, geniculate species of Dalman, viz. *Leptaena rugosa* (see Spjeldnaes 1957 : 172) as type species of *Leptaena*.

Until recently most palaeontologists have accepted the Carboniferous form as a true *Leptaena*, differing only specifically from *L. rugosa*, *L. rhomboidalis*, *L. depressa*, etc. although Hall & Clarke (1891 : 280) did observe that " the extreme differentiation of the muscular area as described is even more distinctly exhibited in the forms of the early Carboniferous than in those of the Silurian and Devonian ". During the early part of this century *L. analoga* continued to be thought of as a true *Leptaena;* admittedly Schuchert & LeVene (1929) designated the species as the type of *Leptagonia*, but then promptly described M'Coy's genus as a subjective synonym of *Leptaena*.

In 1947, Miloradovich proposed the genus *Pseudoleptaena* for leptaenids with a pseudospondylium and a cruralium and cited *L. distorta* Sowerby as the type; and in 1952 Sokolskaja erected the genus *Leptaenella* for leptaenids with a ventral pseudospondylium, naming *P. analoga* Phillips as type species. In so doing she was evidently unaware that not only had *P. analoga* been already designated as the type species of *Leptagonia* by Schuchert & LeVene, but also that *Leptaenella* had already been proposed by Fredericks (1918 : 89) for certain Devonian leptaenids that appear to be congeneric with *Leptaena* s.s. Thus, in effect, Russian palaeontologists are recognising the generic validity of *Leptagonia* and the problem becomes one of deciding firstly, if *Leptagonia* is sufficiently distinct from *Leptaena* to warrant resuscitation; and secondly whether *Pseudoleptaena*, as typified by *L. distorta*, is also different enough to be retained.

Some of the more pertinent features that differentiate *Leptagonia* from *Leptaena* are as follows. In *Leptaena* geniculation is like an exaggeration of the anterior ruga so that both valves bend in the same direction, whereas *Leptagonia* is dominantly biconvex as a result of valve growth towards the commissural plane, prior to the strong geniculation. Although the ventral interiors do not greatly differ in general arrangement, the pseudospondylium of *Leptagonia* is an expression of anterior growth of the confining rim of the ventral muscle field away from the floor of the valve and as such is developed more fully than in *Leptaena* (Pl. 3, fig. 28; Text-fig. 7). Anteriorly it is so elevated as to simulate a true spondylium simplex (Text-fig. 8). The superficial pattern of the dorsal muscle fields for *L. depressa* and *Leptagonia* are similar, but it originates in different ways. In *Leptaena* the dorsal adductors were attached directly to the floor of the brachial valve and were surrounded or slightly elevated by normal processes of shell accretion during growth of the shell. The ontogenetic development of the dorsal muscle field of *Leptagonia*, as seen in a series of dorsal interiors varying in width from 3·7 mm. to 60 mm., on the other hand, was intimately connected with two pairs of muscle plates. In the smallest specimens these plates arise from the floor of the valve, a median pair from below the cardinal process extending anteriorly and separated by a deep groove; and a lateral pair arising from the anterior edges of the socket plates and extending anterolaterally to flank the median pair. These plates are only fused to the floor of the valve posteriorly and at their lateral margins (Text-fig. 10) so as to form anteriorly and antero-laterally directed cavities, all of which must have contained folds of the dorsal mantle epithelium during early life. Each pair of plates respectively accommodated the bases of the anterior and posterior adductor muscles. At the same stage of growth, a pair of ridges extended anteriorly from the points of coalescence of the posterior and anterior adductor plates with each other and with the floor of the valve, which continue parallel to the median septum, at a distance of 0·7 mm. on either side of it and for approximately one-half of its length (Pl. 4, fig. 7); they are thought to have defined the *vascula myaria* which probably continued posteriorly along the depression between the anterior and posterior adductor plates. It is also possible that the body wall, separating the visceral and brachial cavities, may have been supported at these ridges.

In brachial valves with the median septum extending anteriorly for a distance of about 9 mm., a considerable amount of shell thickening has taken place. The lobes of the cardinal process had grown ventrally and are separated distally by a notch of variable dimension, containing the median indentation of the chilidium. The rounded pit below the cardinal process is encased in secondary shell obliterating the posterior ends of the adductor plates. (Text-fig. 11). These progressively lost



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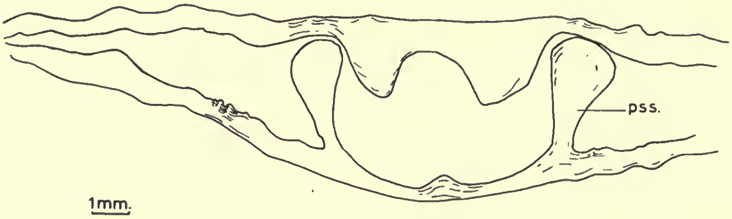

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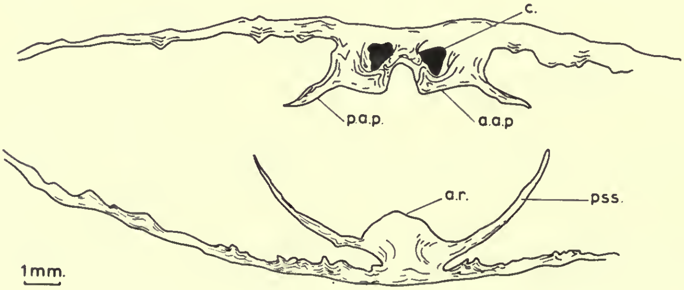

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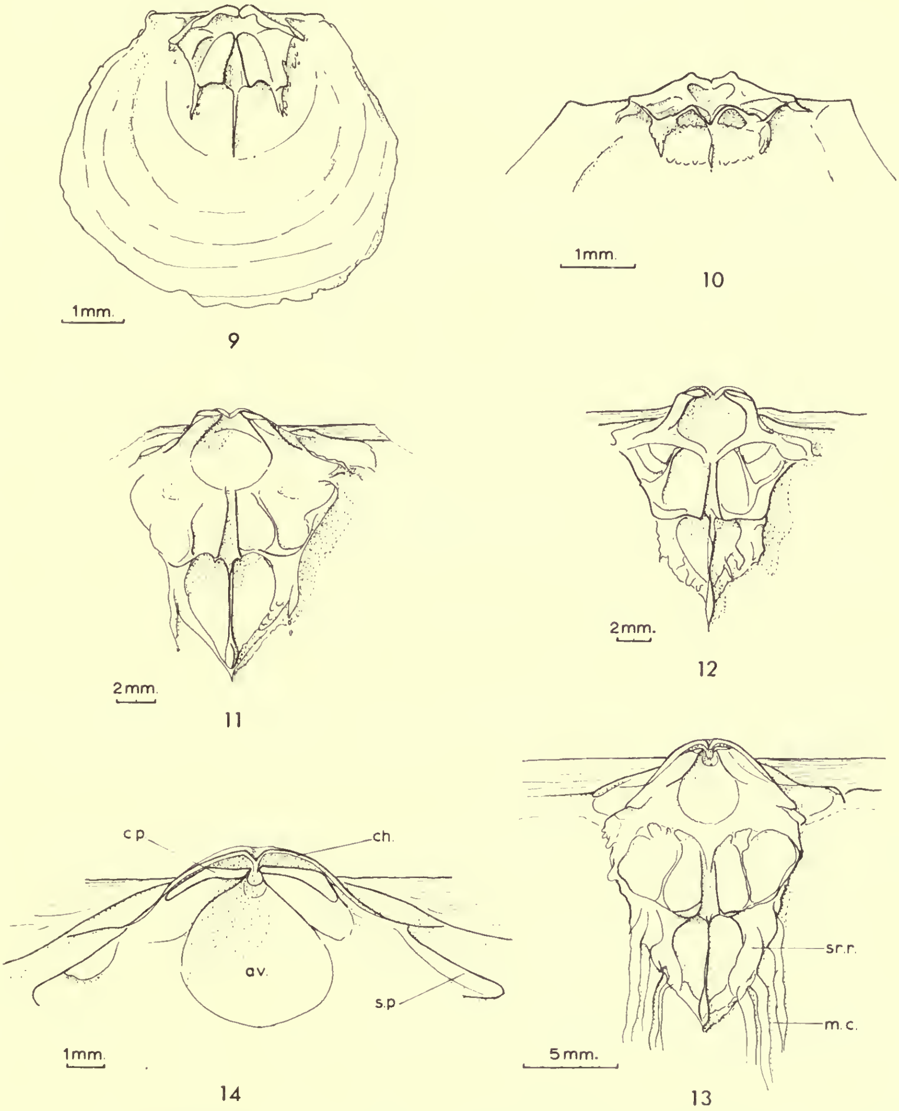
FIGS. 6-8. Illustrations of transverse sections of *Leptagonia analoga* (Phillips) at 2·0 mm., Fig. 6; 3·0 mm., Fig. 7; and 4.5 mm., Fig. 8. from the ventral umbo of a specimen about 30 mm. wide across the visceral disc. *a.a.p*, anterior adductor platform; *a.r*, adductor ridge in pedicle valve; *c*, cavity below dorsal adductor platform; *c.p*, cardinal process; *p.a.p*, posterior adductor platform; *p.f*, pedicle foramen; *pss*, pseudospondylium.

their tent-like shape through infilling of the underlying chambers; presumably during the anterior withdrawal of the mantle epithelium and through secondary shell deposition by the epithelium associated with the muscle bases. Concurrently, the ridges lateral to the median septum became increasingly prominent and thickening



Figs. 9-14. Illustrations of the ontogeny of the brachial valve interior of *Leptagonia analoga* (Phillips) (Figs. 9-13), and details of the adult cardinal process (Fig. 14). All viewed dorsally except fig. 10, viewed postero-dorsally. *ar*, " alveolus ", the subcircular hollow between the bases of the cardinal process; *ch*, chilidium; *c.p*, cardinal process; *m.c*, traces of the mantle canals; *s.p*, socket plates; *sr.r*, ridge surrounding the subrhomboidal region.

occurred between them and the anterior part of the median septum to produce a subrhomboidal structure enclosing the septum anterior to the adductor plates (cf. *Leptaena rhomboidalis*). From the lateral corners of this area small subsidiary ridges extend forward which probably defined the outer edges of the *vascula myaria* trunks. At this stage, the lateral and anterior borders of the adductor plates remain discrete from the valve floor, but the degree of arching seldom exceeds 1 mm. In specimens whose median septum extends 11 mm. from the base of the cardinal process, the posterior adductor plates are generally raised above those associated with the anterior adductor scars (Text-fig. 12). However, this is a temporary feature, as large specimens, with a median septum of 16·5 mm. have both adductor scars at much the same level.

In the largest specimens, the infilling of the chambers below the adductor plates is almost complete, only the lateral margins of the posterior plates showing slight arching. The anterior and posterior scars are less well differentiated, only being separated by a low ridge (Text-fig. 13). The posterior and median borders of the muscle fields are well defined by the continued deposition of secondary shell so as to form a short median ridge extending from the pit between the cradinal process lobes and termininating in the groove between the anterior scars. The subrhomboidal area is well developed and the shell especially thickened round the anterior region of the median septum. The small subsidiary ridges, marking the *vascula myaria* can now be traced anteriorly to where they branch towards the anterior margin of the brachial cavity. By this stage the cardinal process lobes are well separated ventrally and their flat ends are slightly striated for the reception of the dorsal diductor bases. The chilidium had grown ventrally to enclose the posterior faces of the lobes in such a way as to form two cavities from which the diductor muscles extended (Text-fig. 14).

The point of articulation of the valves was always anterior to the interareas, so that during growth the chilidium extended antero-laterally to infill the redundant posterior regions of the sockets. This complicated development contrasts strongly with the simple accretionary processes that were responsible for the differentiation of the dorsal adductor scars of *Leptaena*.

From a provisional investigation of Devonian *Leptaena* in collections from Germany and North America it would seem that internal morphology is intermediate between Silurian *Leptaena* and Carboniferous *Leptagonia*. The Devonian muscle fields are more elevated, especially anteriorly, than those of Silurian specimens, and the cardinal process, with its supporting ridges is comparable to *Leptagonia* in that the myophore bases diverge antero-ventrally to enclose a deep rounded alveolus. The socket ridges are characteristic in *Leptagonia* as they curve smoothly onto the cardinal process rather than being sharply distinct as in *L. depressa* and *L. rhomboidalis*.

In his original description of *L. distorta*, the type species of *Pseudoleptaena*, J. de C. Sowerby (1840 : 10) referred to it as having " A thicker shell than *L. analoga*; well distinguished by its projecting beak, very convex valves, which are not compressed near the beak, and its smaller size." The specimens were collected by Gilbertson from the Isle of Man. This description would be adequate for shells at a stage of development as illustrated in Text-figs. 11 and 12, which are essentially the same as text-fig. 27 of *Pseudoleptaena distorta* in Sarycheva & Sokolskaja (1952 : 37). Thus, the cruralium and pseudospondylium of Miloradovich's genus are developmental stages in the growth of the adult *Leptagonia* and invalidate the retention of *Pseudoleptaena* as a distinct genus.

The mantle canal system of *Leptagonia* differs somewhat from that illustrated for *Leptaena* by Williams (1956 : 274). His illustration shows saccate gonocoels surrounded by major sinus trunks from which are given off numerous peripheral sinuses. In *Leptagonia* it appears that the gonocoels themselves were lemniscate, giving off the periferal sinuses (Pl. 3, fig. 30), with the *vascula media* and *myaria* retained medianly (Text-fig. 15). However, it might be that this condition is only apparent, and could have developed from the pattern illustrated by Williams by the enlargement of the gonocoels so as to have ruptured some of the more peripheral mantle sinuses and their main connecting trunks. Fragments of traces of the mantle canals can be seen throughout most of the thickness of the shell substance and always seem to arise from the edges of the gonocoel, rather than from main vascula trunks, so that it seems unlikely that overgrowth of the gonadial regions has oblitered a former pattern of the mantle canal system. Cvancara (1958 : 861) speaks of " two suboval areas " on either side of the dorsal and ventral muscle fields which he says " appear " to be the only areas of pseudopunctation in *Leptagonia.* It seems likely that the regions to which he refers are the finely papillose areas, here considered as gonocoels (Pl. 4, fig. 2) and that he is incorrect in thinking the teleolae to be confined to those regions. Admittedly, there is a concentration of taleolae in the shell substance antero-lateral of the muscle fields, but they also occur within the shell substance of the muscle platforms and are scattered throughout the rest of the shell. From internal moulds it seems probable that the taleolae were also concentrated more strongly at the base of the trail. The pseudopunctae of *Leptagonia* are inwardly directed flexures of the shell fibres surrounding narrow non-fibrous taleolae so as to produce a closely fitting series of sharp cones, marked internally

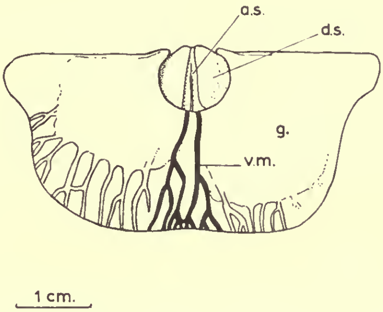


FIG. 15. Illustration of an internal mould of the pedicle valve of *Leptagonia analoga* (Phillips), showing the impressions of the pseudospondylium and mantle canals; *a.s*, scars of adductor muscles; *d.s*, scar of diductor muscles; *g*, gonocoel, with traces of peripheral canals; *v.m*, *vasculum medium* canal traces.

by small tubercles. They were probably formed at the points of attachment of small muscle strands within the mantle, which may have assisted in the circulation or explusion of the gonadial products from the mantle canal system, and in the movement of the mantle edges. Such an interpretation might explain the concentration of taleolae in the gonadial regions, and at the base of the trail.

An unusual feature seen rarely in pedicle valves is the development of two slight conical thickenings of the shell symmetrically placed between the pseudospondylium and the anterior margin of the disc. Similar, though more papillose humps are to be seen in some Silurian leptaenids, and may indicate that the spirolophe was slightly conical and directed towards the dorsal valve.

Longitudinal sections of young shells, of hinge-width approximately 2·5 cm. show an open supra-apical pedicle foramen. A study of the shell texture shows the canal through the shell to be lined with fibres disposed parallel to the canal surface and more or less normal to the ventral, external, surface of the valve, an area which must have been covered by chitin (Text-fig. 16). In describing his Australian specimens of cf. *L. analoga* Cvancara (1958 : 860) apparently noted the same feature for he states that " The foramen appears to be lined with a tubular sheath ". The disposition of these fibres and their inferred relationship to the epithelium which secreted them is obscure, but it would seem likely that they were deposited during the withdrawal of the outer epithelium following the development and redundancy of the nepionic pedicle sheath (Arber 1939 : 84). Outer epithelium must have extended through the nepionic shell to have formed the pedicle sheath. During subsequent growth the withdrawal of the outer epithelium resulted in the deposition of fibres parallel to the pedicle canal and also drew its junction with the pedicle epithelium inwards, so lining the canal with chitin. Spaces within the shell substance, parallel to these fibres, suggest that there might have been periodic advance and retraction of the outer epithelium to pedicle epithelium boundary.

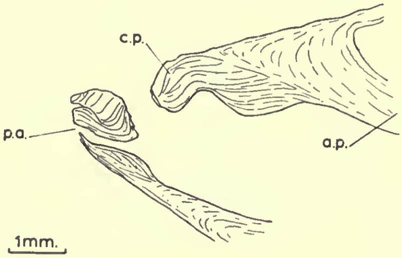


Fig. 16. Illustration of a median longitudinal section through a young shell of *Leptagonia analoga* (Phillips) showing the cavity below the dorsal adductor platform, thickening anterior to the cardinal process and the pedicle aperture with its lining of secondary fibrous calcite; *a.p*, adductor platform; *c.p*, cardinal process; *p.a*, pedicle aperture.

In 1958 Cvancara came to the same conclusions about the reintroduction of *Leptagonia* as the correct generic name for the distinctive Carboniferous leptaenids. He bases his reasoning upon a study of the ventral valves in which he observed the muscle field to be supported upon a " well-developed spondylium ", in contrast to the flat muscle field of *Leptaena*. Cvancara did not examine the type specimen of *L. analoga*, but there can be little doubt that the upper Tournasian specimens from New South Wales which he describes are closely comparable with Phillips' species.

Leptagonia analoga (Phillips)

(Pl. 3, figs. 26–31. Pl. 4, figs. 1–9. Text-figs. 6–17)

1836 *Producta analoga* Phillips: 116, pl. 7, fig. 10.
1844 *Leptagonia analoga* (Phillips) M'Coy: 117.
1861 *Strophomena rhomboidalis* var. *analoga* (Phillips) Davidson: 119, pl. 28, figs. 1–6, 9–13.
1958 *Leptagonia* cf. *L. analoga* (Phillips); Cvancara: 860, pl. 100, figs 6–13.

DIAGNOSIS. Subquadrate to semicircular *Leptagonia* with adult disc about one-half as long as wide, outline commonly modified by emargination medianly and less commonly laterally; immature shells plano-convex, adult shells biconvex, about one-half as deep as long, commonly uniplicate, rarely parasulcate; dorsally directed trail variably developed; visceral region with 14–18 regular rugae having mean wave-lengths of 1·0 mm. and 1·4 mm. for the fifth and tenth rugae; rounded costae, commonly 5 or 6 in 2 mm., 10 mm. antero-medianly of umbones; pseudospondylium subcircular, seven-tenths as long as wide and about one-third as long as length of disc; dorsal muscle field one-half as long as wide. median septum extending forward for about two-fifths length of disc.

MEASUREMENTS (in mm.)

		length	width
LECTOTYPE.	Complete eroded specimen (B.8963)	*c.* 20	*c.* 44
	Incomplete pedicle valve (L.3817/1)	32	*c.* 50
	Incomplete brachial valve (BB.52731)	—	*c.* 54
	Complete brachial valve (BB.52730)	6·0	*c.* 6·9
	Internal mould (BB.55777)	30	*c.* 45
	Complete shell (BB.52729)	*c.* 5·0	5·5

LOCALITIES AND HORIZONS: Lectotype from Bolland, Yorkshire. B.8936 (Pl. 3, figs. 26, 27).

L.3817/1 from the Caldwell Collection, Hunterian Museum, Glasgow, collected from the Lower Carboniferous of Carrick-on-Shannon, Counties Leitrim and Roscommon, Ireland.

BB.55777 Gilbertson Collection, probably from the Lower Carboniferous of the Isle of Man.

BB.52729–30. The subreefal limestones and shales of Bunnahone, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. Low. D. zone.

B..52731. The Ballyshannon limestone of Streadagh Point, Co. Sligo, Ireland S_2.

DISCUSSION. There is considerable variation of outline and in the length of visceral disc at which geniculation took place, so that the number of rugae on the ventral discs of nineteen specimens from Carrick-on-Shannon ranges from 13 to 23. The wave-lengths of the fifth and tenth rugae from the umbo varies from 0·8 mm. to 1·1 mm. (mean 1·0 mm.) and from 1·1 mm. to 1·6 mm. (mean 1·4 mm.), on 15 specimens. Costation was little affected by the point at which geniculation occurred and remains with 3, 6, 4 and 3 specimens having respectively 4, 5, 6 and 7 costae per 2 mm. width at 10 mm. antero-medianly from the ventral umbo. Almost invariably the trail is depressed medianly, commonly also affecting the anterior margin of the disc to form a uniplicate commissure. Those shells which geniculated before the more usual disc length of about 27 mm. may be slightly depressed laterally as well as antero-medianly (cf. Davidson 1861, pl. 28, fig. 7). Such shells have been separated as *L. distorta*, but within large samples no satisfactory separation from *L. analoga* can be established. All contain the same internal structures at various stages of development, and the length at which the trail developed ranges from typical *L. distorta*, about 15 mm. long, to full sized specimens of *L. analoga*. It is necessary

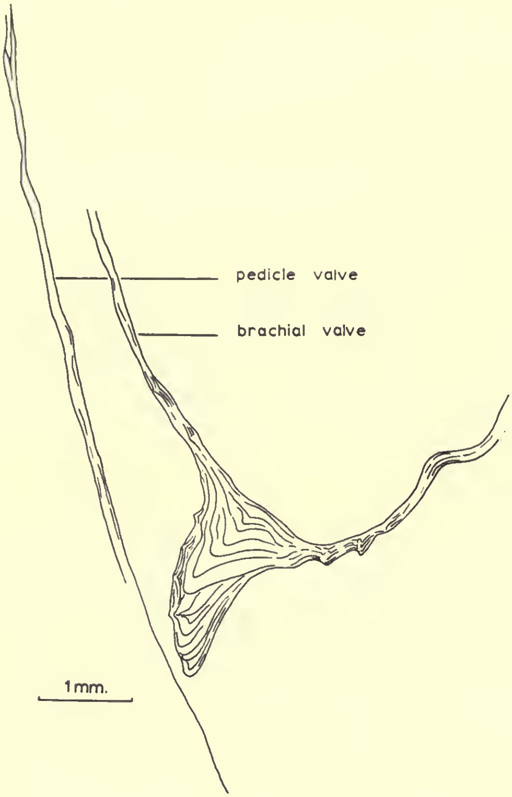


FIG. 17. Illustration of the anterior region of a median longitudinal section through the shell of *Leptagonia analoga* (Phillips) showing the secondary marginal ridge around the visceral region of the brachial valve, developed at the point of geniculation. The brachial cavity is to the right on the illustration.

to discover whether valid stratigraphic or facies differences occur within these forms before being at all sure of their taxonomic positions.

Irregularly concentric fine growth lines are continued on the trail, while the traces of the mantle canal system can also commonly be seen within the shell substance below every second or third rib. The rugae are not continued on to the trail.

The ridge around the adult dorsal visceral disc is of secondary shell material and becomes increasingly prominent through adulthood. (Text-fig. 17).

Only a few specimens of *L. analoga* were found among the etched material from Co. Fermanagh, but the author has made use of specimens in the Caldwell Collection from Carrick-on-Shannon, about 36 miles S.S.W. of Derrygonnelly, kindly lent by the Hunterian Museum, Glasgow. Measurements on 10 brachial valve interiors from this collection shows that the length of the median septum, measured from the posterior margin of the adductor field, is consistently similar to the total width of the socket ridges ($r = 0{\cdot}924$).

Superfamily **DAVIDSONIACEA** King 1850

Family **ORTHOTETIDAE** Waagen 1884

Subfamily **ORTHOTETINAE** Waagen 1884

[= Derbyoidinae Thomas 1958]

Genus ***BROCHOCARINA*** nov.

1855 *Leptaena* (*Strophomena*) M'Coy: 450 (pars).

1861 *Streptorhynchus* King 1850: Davidson: 123 (pars) pl. 26, figs. 5 (?2 and 6) *non* Figs. 1, 3 and 4.

1910 *Schuchertella* Girty 1904; Thomas: 126.

1930 *Schuchertella* Smyth: 555, pl. 15, figs. 5–9.

DIAGNOSIS. Thin plano-convex Orthotitinae with entire chilidium; dental ridges deep, fusing posteriorly in ventral apex with trifid ridges enclosing lanceolate adductor scars.

DESCRIPTION. Outline subsemicircular, profile more or less plano-convex with narrow body cavity; ventral interarea long, apsacline, with arched pseudodeltidium, perideltidium variably defined; dorsal interarea and chilidium reduced; radial ornament parvicostellate with costellae regularly intercalated; teeth strong, continued at delthyrial margins as obliquely disposed posteriorly prominent dental ridges; ventral muscle field defined only in adult shells, adductor scars lanceolate, inserted posteriorly between low trifid ridges, diductor scars flanking and spreading anteriorly; cardinal process low, lobes well separated by sulcus with median chilidial ridge; socket plates at about 20° to hinge-line, slightly recurved; adductor field obscurely impressed, apparently flabellate to subcircular and separated by slight median ridge in adult shells; shell substance irregularly pseudopunctate.

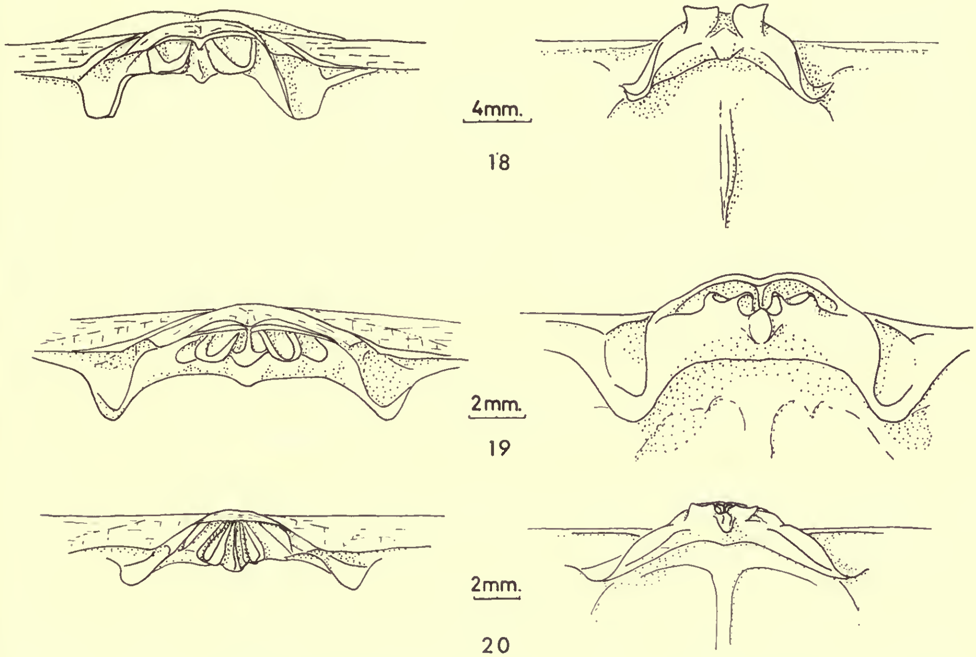
TYPE SPECIES. *Schuchertella wexfordensis* Smyth 1930.

DISCUSSION. The new genus *Brochocarina* conforms to the requirements of the family Orthotetidae Waagen 1884, in having a low cardinal process and ventral interior with a low median septum continuous with the inside of the pseudodeltidium and fused to the dental ridges. At subfamilial level the distinction between Orthotetinae Waagen, and Derbyiinae Stehli, is based upon the form of the socket plates; those genera with widely divergent socket plates, which tend to recurve towards the posterior margin as they fuse to the dorsal valve floor, being placed in the Orthotetinae, while those genera with less widely divergent socket plates, fusing to the floor without curvature, being assigned to the Derbyiinae. The genus possesses somewhat recurved socket plates, an ill-defined dorsal adductor field, greatly reduced dorsal interarea and small chilidium and is therefore assigned to the Orthotetinae.

The genera comprising the Orthotetinae are distinguished by differences in their ventral interiors, the form of the cardinal process lobes and the shell profile. *Brochocarina* differs from *Orthotetes* Fischer de Waldheim (? *Werriea* Campbell 1957) in having a less highly developed ventral median septum which has never been observed to have fused with the dental ridges posteriorly to such an extent as to have formed a delthyrial chamber (The " spondylium " of early authors and " secondary spondylium " of Thomas 1958 : 9). *Hipparionyx* Vanuxem is clearly distinguished by its subcircular outline, strongly impressed ventral interior and high, strongly divergent cardinal process lobes.

A comparison of the original descriptions of *Derbyoides* Dunbar & Condra (1932 : 114) and *Tapajotia* Dresser (1954 : 33) suggests that these genera are less distinctive than was thought by Thomas (1958 : 21) or by Dresser himself. While admitting " that *Tapajotia* is closely related to *Derbyoides* " Dresser separates the two largely on his mistaken belief that *Derbyoides* possesses a strong ventral median septum. In fact Dunbar & Condra (1932 : 115) state that " A median septum is present but rather weak and low, extending not over one-third the distance to the front of the valve ", and inspection of their pl. 9, fig. 13 confirms this statement. For the above reasons Campbell (1957 : 46) states that *Tapajotia* " is probably a synonym of *Derbyoides* ". This conclusion was arrived at by Mendes (1958 : 317, 319) in his review of the Tapajos River fauna of the Amazon Valley, and is supported by Cooper (personal communication). However, having studied topotypic material of *Derbyoides* and *Tapajotia* the writer is of the opinion that the two genera are distinctive and worthy of separation from *Brochocarina* gen. nov., while all three were probably closely related and derived from a schuchertellid stock.

The distinction between *Derbyoides* (Pl. 4, figs. 10–14) and *Tapajotia* (Pl. 4, figs. 15–23) include the following features. The brachial valve of *Derbyoides* is " strongly and rather evenly convex, with the highest point near the mid-length ", (Dunbar & Condra 1932 : 115) and the valves are commonly faintly medianly sulcate in contrast to the plane, posteriorly flattened valves of both *Tapajotia* and *Brochocarina*. Dresser is mistaken in describing the widest part of *Tapajotia* as being " anterior " to the transverse mid-line. His illustrations, and the material at hand, show the greatest width to be at one-third the shell length, and the hinge-line width to be nine-tenths of this width. The greatest width of *Derbyoides* is at mid-length and the hinge-line is only three-quarters this width. The dorsal interiors differ in that a short median septum is developed between and anterior to the clearly impressed adductor scars of *Derbyoides*, neither of which are seen in *Tapajotia*, and its cardinalia are more massive, extending for one-third of the hinge-line width as compared to one-quarter the width in *Tapajotia*. The ventral adductor scars are similar, but differ in being more elongately lozenge-shaped in *Derbyoides*, those of *Tapajotia* having more or less parallel lateral margins bordered by slight ridges. The delthyrial angle is about 20° greater in *Derbyoides* than in *Tapajotia* or *Brochocarina*, and its shell substance is much thicker and led to the development of marginal ridges around the edges of both valves.



Figs. 18-20. Illustrations comparing the cardinalia of *Derbyoides* Dunbar & Condra (Fig. 18), *Tapajotia* Dresser (Fig. 19), and *Brochocarina* gen. n. (Fig. 20) in posterior (on the left) and internal (on the right) views.

Brochocarina is distinguished from both *Derbyoides* and *Tapajotia* primarily by reason of its ventral interior. The teeth of the American genera are traced along the edges of the delthyrium as low ridges which do not fuse at the beak of the valve to form a ventral median septum. The teeth of *Brochocarina* are supported by distinct dental ridges, strongly differentiated from the inner surface of the interarea. In adulthood these ridges reached almost to the valve floor and throughout life they fused posteriorly and gave rise to the tripartite median septum that separated and enclosed the lanceolate adductor scars (pl. 5, figs. 8, 13).

The dorsal cardinalia is similar to that of *Tapajotia*, but differs in that the socket plates diverge at 20° to 25° from the hinge-line instead of at about 35° in the Brazilian and Nebraskan genera (Text-figs. 18–20). The outline of *Brochocarina* tends to be more semicircular than that of the other genera, as its maximum width is commonly at the hinge-line. The plano-convex profile is like that of *Tapajotia* but different from the dorsi-biconvex profile of *Derbyoides*. The external radial ornament, with about 11 ribs in 5 mm. at 10 mm. antero-medianly of the dorsal umbo, is of much the same frequency as that of the American genera. However, the form of the ribbing does vary. *Brochocarina* is parvicostellate with narrow, rather angular ribs which only attain their full dimensions after about 5 mm. (First order costellae attain full size after 3 or 4 mm. while second and third order costellae only attain full size after about 10 mm., if at all.) This led to the development of relatively wide interspaces, especially posteriorly, and this contrasts with the more regular, rounded radial ornament of the other two genera.

Thus, *Brochocarina* may be distinguished principally by its ventral interior and narrowly divergent socket plates. *Derbyoides* differs in its convex and heavily thickened brachial valve and in having a medianly developed dorsal septum. The Fermanagh shells are older than the other genera of the subfamily, except for *Hipparionyx*, and yet show a stage of development of the ventral interior apparently intermediate to that of *Tapajotia* and *Orthotetes*. Of the presently described genera *Brochocarina* could have been ancestral to *Derbyoides* and *Tapajotia* by the reduction of the dental ridges in these later genera, and to *Orthotetes* by the increased deposition of secondary shell in this region.

Brochocarina wexfordensis (Smyth)

(Pl. 4, figs. 24–26, Pl. 5, figs. 1–23. Text-figs. 18–26)

1855 ?*Leptaena* (*Stromphomena*) *crenistria* (Phillips); M'Coy: 450.
1861 *Streptorhynchus crenistria* (Phillips) Davidson (pars): 124, pl. 26, fig. 5, (?2 and 6) *non* figs. 1, 3 and 4.
1930 *Schuchertella wexfordensis* Smyth: 555, pl. 20, figs. 5–9.
1931 *Derbyia ambigua* Muir-Wood (pars): 144, fig. 3, *non* pl. 10, figs. 4, 5.

DIAGNOSIS (emended). Outline subsemicircular, with length about two-thirds maximum width; radial ornament unequi-parvicostellate with about 6 ribs in 2·5 mm. width, 5 mm. antero-medianly from dorsal umbo, interrupted by occasional growth lamellae, growth-lines numerous; pseudodeltidium arched with apical angle about 65°, flanked by wide perideltidium with apical angle about 130°, teeth prominent, adult dental ridges deep, almost reaching floor of valve; socket plates low, about one-quarter hinge width, recurving posteriorly to floor of valve.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete brachial valve (T.C.D.196/1086)	36·3	*c.* 49·6
PARATYPE.	Incomplete pedicle valve (T.C.D.199/1086)	—	63·5
	Incomplete pedicle valve (BB.52732)	—	67·9
	Incomplete pedicle valve (BB.52734)	*c.* 11·0	—
	Incomplete brachial valve (BB.52735)	—	*c.* 9·5
	Complete brachial valve (BB.52736)	32·3	*c.* 53·0
	Complete crushed shell (BB.52738)	*c.* 64·0	*c.* 90·0

LOCALITIES AND HORIZONS: Holotype and paratype: Smyth Collection Nos. 196/1086, 199/1086 at Trinity College, Dublin, collected from Lower Carboniferous rocks on the west side of Hook Head, Co. Wexford. ?C_1.
BB.52732–52736: Subreefal limestones and shales of Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1. BB.52738: Bundoran shales, Bundoran, Co. Donegal. S_2.

DISCUSSION. In all known respects the present Fermanagh material agrees with the type specimens of *Schuchertella wexfordensis* Smyth, 1930, from upper Tournaisian and lower Viséan beds of Hook Head, Co. Wexford. Although a statistical comparison of the growth axes " a " for the Hook Head and Fermanagh specimens indicates that there is a slight significant difference ($0{\cdot}02 < p < 0{\cdot}05$), the ventral interiors are identical (cf. Pl. 4, fig. 24 with Pl. 5, fig. 13) and no differences can be distinguished between the external ornamentation. The two are, therefore, considered to be conspecific.

In 1931 Muir-Wood (in Garwood) described a new species of davidsoniacean, *Derbyia ambigua*, from C_2 beds in Roxburghshire. Five of the original specimens are in the British Museum (Nat. Hist.), but they are not all conspecific and two (B.56425, B.56410) are thought to be conspecific with Smyth's species while a third fragment (B.56415) is probably conspecific. The holotype of *D. ambigu* (B.56411) and the pedicle valve interior (B.56416) figured (1931, pl. 10, fig. 5) are distinctive. Without brachial valve interiors it is difficult to be certain about the generic designation, but the high ventral median septum and small delthyrial cavity are more reminiscent of *Orthotetes* than *Derbyia*.

The description of *Leptaena* (*Strophomena*) *crenistria* (Phillips), given by M'Coy in 1855 (: 450) is in agreement with the present species in all recorded features. However, it is not conspecific with *Spirifera crenistria* Phillips (1836 : 216) which has a convex brachial valve (pl. 9, fig. 6) and is assigned correctly by Thomas to *Schellwienella* (1910 : 126). The illustration of *Streptorhynchus crenistria* (Phillips) by Davidson (1861, pl. 26, fig. 5) has been variously ascribed; to *Schuchertella* by Thomas (1910) and Smyth (1930 : 555), and to *Tapajotia* by Dresser (1954 : 37). Dresser considered Davidson's specimens to be " specifically distinct from *T. tapajotensis* because they possess a much deeper impression of the muscle scars in both valves ". This observation could be used to separate the present species from that illustrated by Davidson. It should be remembered, however, that his specimen illustrated in fig. 5 is from Hook Head, the type locality, and that several of Davidson's illustrations are somewhat stylized. It may be that Davidson's figs. 2 and 6 (cf. pl. 26) are also conspecific.

The species differs from *Schuchertella pseudoseptata* Campbell (1957 : 46), described by him as closely resembling *S. wexfordensis*, by not having socket plates which are parallel to the hinge-line. Campbell's species apparently never reached the dimensions of *S. wexfordensis*, and from the description is only comparable in its ventral muscle field and septation.

Growth of the shell was almost equally radial to give a high coefficient of correlation between length and width ($r = 0{\cdot}998$). The greatest width is almost invariably at the hinge-line, so that the cardinal extremities remain at 90° or less. Costellation is probably a reflection of setal growth at the mantle margin, and as such remains constant throughout several genera of the davidsoniaceans. As in other genera, the costae number sixteen to eighteen on each valve, one to four orders of costellae being regularly and symmetrically intercalated so that in a width of 2·5 mm. anteromedianly of the dorsal umbo the costellae are arranged as in Table 8. Because of the flatness of these shells, and the frequency with which their anterior margins are broken, the best estimate of shell thickness is gained by measuring the height of the delthyrium (Table 11). From the complete specimens available it is clear that this posterior region represents the region of greatest shell depth.

Fine growth lines form minute ridges across the crests of the costellae which became increasingly prominent anteriorly, until in adult shells, the ridges are prolonged into small spinose lamellae Pl. 5, fig. 12. Concentric lamellae, formed by interruptions in growth, are variably developed, although they tend to be concentrated towards the adult shell margins, presumably because of reduced shell growth.

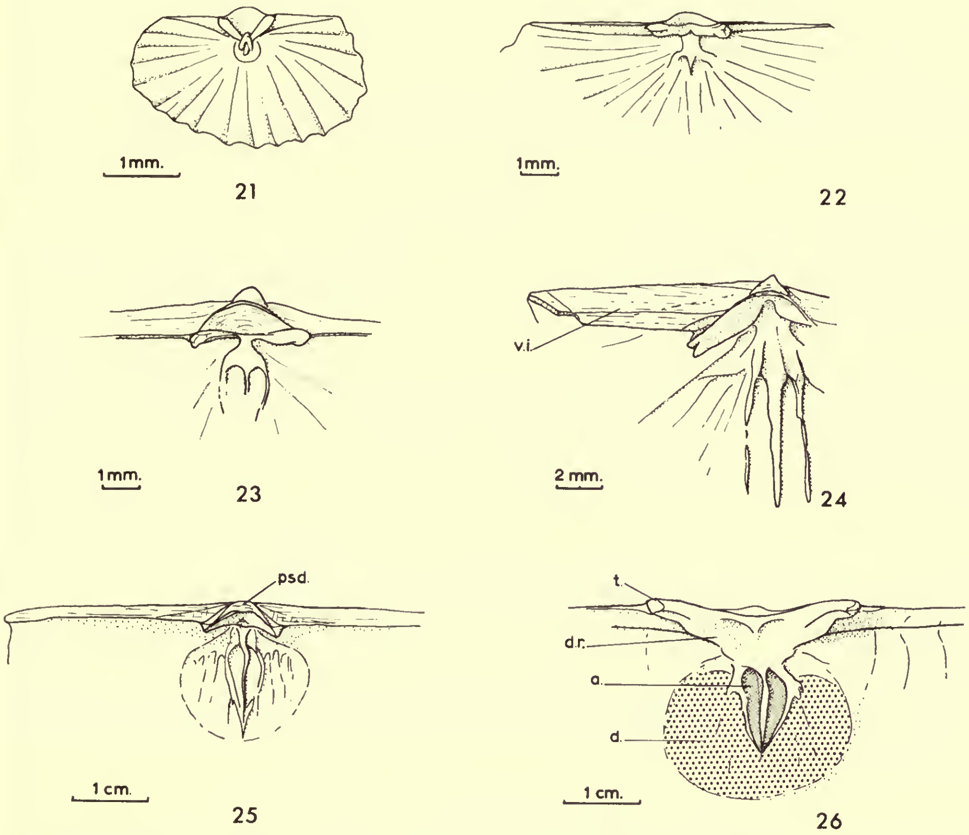
An unusual characteristic of the species, is the way in which the brachial valve commonly becomes flat, or slightly concave, over a distance of about 10 mm. immediately anterior to the initial convexity of the umbonal region. The perideltidium, which is best seen on calcareous shells (Pl. 5, fig. 19), extends laterally for about one-half the width of the ventral interarea and is finely striated vertically, as well as bearing the sporadic growth lines that traverse the whole interarea and pseudodeltidium. It is possible that a similar area occurs upon the dorsal interarea. Clearly the periostracal shell covering was differentiated in the perideltidial region and the fine vertical striations are suggestive of a tight bonding to the shell surface, as might be expected under a periostracal pad (Williams 1956 : 257).

The chilidium is best seen in adult shells, (Pl. 5, figs. 6, 18) but its development can be followed from shells only about 3 mm. wide. In adult shells, with a dorsal interarea 1·5 mm. long, the chilidium curves around the base of the cardinal process lobes and is separated from them laterally by prominent grooves. A short chilidial ridge supports the structure between the cardinal process lobes and laterally it merges with the socket plates.

Internally, the margins of adult shells are commonly secondarily thickened to a greater extent than the remaining surfaces, but never to the extent of those of *Derbyoides nebrascensis*. This thickening, together with the closely spaced external lamellae it the shell margin, indicates periodic mantle retraction. This process increased both the thickness of shell substance and the total depth of the shell without appreciable increase to shell length or width.

The development of the dental and median ridges is informative in indicating the affinity of these shells with stratigraphically younger forms, and helps to confirm the interpretation by Williams (1965 : H404) of the delthyrial chamber of *Orthotetes* Fischer de Waldheim. The low trifid median ridge, which separates the ventral adductor scars from the diductor scars, arose umbonally and fused with the posterior ends of the dental ridges as a result of secondary shell deposition (Text-figs. 21–26). Shell deposition in adult stages increased the depth of the dental ridges until they approached the floor of the valve posteriorly (Text-fig. 26). Continued shell deposition umbonally could have buried the posterior ends of these ridges, together with the median ridge, so that in cross-section the ventral beak might appear to possess a thick " pseudospondylium ".

A study of dorsal interiors varying from 1·5 mm. to 55 mm. wide shows certain changes in the cardinalia. The angel of the socket plates to the hinge-line varies, tending to decrease slightly with age. In an assemblage of variously sized shells the angle is commonly between 20° and 25°. The smallest shells show scarcely any interarea, the cardinal process is but slightly differential into two lobes, the socket plates are straight, (Pl. 5, figs. 20, 21) and there are only the slightest lateral swellings indicating the origins of the chilidium. By a width of 4·5 mm. all the essential elements of the cardinalia are distinguishable, save for the median ridge and ventral node between the cardinal process lobes and the slight thickening between the socket plates, bounding the postero-median edges of the subcircular adductor field (Pl. 5, fig. 22).



21 22 23 24 25 26

FIGS. 21-26. Illustrations of the ontogeny of the pedicle valve interior of *Brochocarina wexfordensis* (Smyth), postero-ventral aspect, showing the fusion of the dental ridges with the median septum. *a*, adductor scar; *d*, diductor scar; *d.r*, dental ridge; *psd*, pseudodeltidium; *t*, tooth; *v.i*, ventral interarea.

TABLE 8

No. of ribs	4	5	6	7	8
A	0	4	6	3	3
B	2	5	3	1	0

TABLE 8. The number of ribs counted in 2·5 mm. at 5 mm. (A) and 10 mm. (B) anteromedianly of the dorsal umbo of *Brochocarina wexfordensis* (Smyth).

TABLE 9

$\bar{l}$ mm. (var.) = 6·33 (77·093)
$\bar{w}$ mm. (var.) = 10·03 (213·866)
r = 0·998
a (var.) = 1·666 (0·00111)

$\bar{w}$ mm. (var.) = 10·03 (213·866)
$\bar{s}$ mm. (var.) = 2·63 (8·032)
r = 0·997
a (var.) = 0·194 (0·000023)

TABLE 9. Statistics of length (l), maximum width (w) and maximum width of the socket plates (s) of 12 dorsal valves of *Brochocarina wexfordensis* (Smyth) from Co. Fermanagh.

TABLE 10

$\bar{l}$ mm. (var.) = 26·60 (70·203)
$\bar{w}$ mm. (var.) = 38·61 (137·950)
r = 0·983
a (var.) = 1·402 (0·01114)

TABLE 10. Statistics of length (l) and maximum width (w) of 8 pairs of measurements from type dorsal valves of *Brochocarina wexfordensis* (Symth) from Hook Head, Co. Wexford.

TABLE 11

$\bar{l}$ mm. (var.) = 9·56 (122·115)
$\bar{w}$ mm. (var.) = 12·96 (226·31)
r = 0·994
a (var.) = 1·361 (0·00079)

$\bar{l}$ mm. (var.) = 9·56 (122·115)
$\bar{h}$ mm. (var.) = 1·29 (1·652)
r = 0·956
a (var.) = 0·116 (0·00042)

$\bar{h}$ mm. (var.) = 1·29 (1·652)
$\bar{d}$ mm. (var.) = 1·83 (3·873)
r = 0·984
a (var.) = 1·531 (0·00268)

TABLE 11. Statistics of length (l), maximum width (w), height of delthyrium (h) and width of delthyrium (d) at the anterior margin of the interarea of 16 pedicle valves of *Brochocarina wexfordensis* (Smyth) from Co. Fermanagh.

?*Orthotetinid* gen. and sp. indet.

(Pl. 7, figs. 1–7)

Three distinctive cardinalia have been recovered from the etched limestones of the Sillees River, Bunnahone, but no pedicle valves are known. Fortunately the three vary in size, viz. total widths of socket plates = 4·7 mm., 14·1 mm. and 17·6 mm., allowing ontogenetic changes to be observed. These cardinalia are quite unlike other davidsoniacean species from the faunas and are unusual in their slight strophomenacean characteristics, i.e. external ornament and strong dorsal median septum. A cardinalia figured by Davidson (1861, pl. 27, figs. 6, 7) from Settle, Yorkshire is probably conspecific, but was included as *Streptorhynchus crenistria;* otherwise comparable material does not appear to have been described.

The brachial valve was apparently gently convex with a wide straight hinge-line, well developed anacline interarea and arching chilidium from below which the cardinal process projected strongly. The external ribbing occurs with a frequency of about 10 ribs in 5 mm. width, 5 mm. from the umbo, and is apparently parvicostellate. Between the ribs is a less distinct concentric ornamentation of minute ridges (Pl. 7, fig. 1), similar to that of strophomenaceans.

Internally the cardinal process is typically davidsoniacean with two well developed incised lobes between which is a chilidial ridge terminating ventrally in a node. The socket plates are strongly recurved and nearly parallel to the interarea; medianly they merge to the cardinal process and prominent median septum, which is present even in the smallest specimen.

The lack of pedicle valves make it impossible to be quite sure of familial placing but the form of the socket plates indicates either the Schuchertellinae or Orthotetinae as the most likely subfamilies. Of these the latter group seems more appropriate as some members of the Orthotetinae have a poorly developed dorsal median septum. Until more material is available, in particular matching pedicle valves, a full generic or specific designation will not be attempted.

Family **SCHUCHERTELLIDAE** Williams 1953

Subfamily **SCHUCHERTELLINAE** Williams 1953

Genus ***SERRATOCRISTA*** nov.

DIAGNOSIS. Shell small, commonly ventribiconvex, pedicle valve strongly curved to conical in young shells; hinge-line straight, commonly approximating to maximum width; ventral interarea elongate, apsacline to catacline, pseudodeltidium arched and entire, perideltidium obscure; dorsal interarea and chilidium much reduced; radial ornament multicostellate, spinose with costellae regularly intercalated; teeth supported by low dental ridges; muscle scars indistinct, rarely with slightly raised lanceolate adductor scars; cardinal process low, bilobed and supported by widely divergent socket-plates at about 25° to hinge-line; adductor field obscure, shell substance probably pseudopunctate.

TYPE SPECIES. *Serratocrista fistulosa* sp.n.

DISCUSSION. *Serratocrista* is included in the subfamily Schuchertellinae on account of its typically schuchertellid dorsal interior, including socket plates which diverge from the hinge-line acutely and which recurve slightly at their antero-lateral extremities. This is in contrast to the socket plates typical of the Streptorhynchinae, which diverge from the hinge-line less acutely, at 50° to 60°, and continue antero-laterally fused to the brachial valve floor with no recurvature towards the posterior margin. *Serratocrista* differs from *Schuchertella* Girty, in being pseudopunctate and having no dorsal median ridge, features which recall *Orthopleura* Imbrie, although it differs from this genus in being multicostellate and " spinose". Unlike *Schuchertellopsis* Maillieux, representatives of the new genus were not completely cemented by their pedicle valves to a foreign body during their life.

Serratocrista fistulosa sp.n.

(Pl. 6, figs. 1–12)

DIAGNOSIS. Biconvex Schuchertellinae bearing spinose, strong ribs; chilidium obsolescent, weak dental ridges and poorly impressed muscle scars.

DESCRIPTION. Outline transversely semi-oval, approximately two-thirds as long as wide; biconvex, one-third as thick as long, slight dorsal median sulcus; strongly multi-costellate bearing about four crestal " spines " medianly between 9 and 10 mm. from dorsal umbo. About eight ribs occur per 2·5 mm. width antero-medianly at 5 mm. from dorsal umbo, pedicle valve costae commonly slightly stronger than costellae; ventral adductor scars posteriorly placed, lanceolate, enclosed by slight ridges; cardinal process low, lobes well separated by sulcus, socket plates diverge from hinge-line at about 25°, prominent anteriorly, reaching almost one-third width of hinge-line; sockets arched postero-medianly by antero-lateral growth of vestigial chilidial plates; median septum absent, adductor scars obscure.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52739)	14·4	18·0
PARATYPES.	Complete brachial valve (BB.52740)	9·6	14·6
	Complete pedicle valve (BB.52741)	14·1	20·0
	Complete pedicle valve (BB.52744)	3·6	5·1

TYPE LOCALITY. Sillees River, about 300 yds. east of Bunnahone Lough (low D zone).

DISCUSSION. The costellate ornamentation is distinctive with its short pointed " spines " commonly arising alternately from the crests of the ribs (Pl. 6, fig. 3). These " spines " become slightly more widely spaced anteriorly, but medianly between 9 and 10 mm. from the umbo there are about four. Costellae were added by branching and intercalation, although the latter is rare on pedicle valves and the branching is predominantly median in origin. The costellae approximate to the size of the costae within about 5 mm. of their origin. At 5 mm. from the umbo 3, 3 and 9 valves have 6, 7 and 8 ribs per 2·5 mm. width antero-medianly. The ribbing is prominent with rounded crests and straight or slightly concave sides, up which fine growth-lines can be traced (Pl. 6, fig. 3), and both wave-length and amplitude of the ribs are commonly about equal. The radial ornamentation is comparable to that of the mid Devonian European species *Xystostrophia umbraculum* (Schlotheim); both species developed spinose outgrowths from their ribs, but in other respects, such as cardinalia, the two are quite distinctive.

The shell interiors are unusually featureless, despite secondary thickening; the dental ridges show no accentuation with increased age, nor is there any sign of a median ridge in either valve.

Although described as pseudopunctate, the shell structure is a little uncertain. The internal surfaces, of pedicle valves in particular, are covered by small pits which are confined neither to ribs nor interspaces. Unfortunately, unsilicified material is not available so microscopic examination of unaltered shell is impossible. One incompletely silicified specimen is broken across the ventral interarea and part of the valve. The inner and outer surfaces are completely silicified but internally there is only a silica lattice comprising lamellae held by more or less perpendicular fine rods (Pl. 6, fig. 11). This structure may be interpreted as being selective silicification along planes in the original shell structure which represented a form of punctation and the shell lamellae. Thomas (1958) describes Permian *Streptorhynchus* from Western Australia as having a shell structure that differs from his other Davidsoniacea. The conical flexures of the shell lamellae are directed outwards, rather than inwards as in normal pseudopunctate shells, and Thomas suspects that these flexures surrounded a fine canal (Thomas 1958, pl. 19). In the Australian material this " punctation " was confined to the ribs, as is the internal punctation of many enteletaceans and terebratuloids.

If the shell structure of the Fermanagh material was comparable it would explain the minute pits on internal surfaces and could explain the selective silicification of the shell figured in Plate 6, fig. 11.

TABLE 12

$\bar{l}$ mm. (var.) = 10·83 (17·530)
$\bar{w}$ mm. (var.) = 14·52 (31·078)
r = 0·970
a (var.) = 1·332 (0·0262)

$\bar{l}$ mm. (var.) = 10·83 (17·530)
$\overline{th}$ mm. (var.) = 3·02 (0·654)
r = 0·893
a (var.) = 0·193 (0·0022)

TABLE 12. Statistics of length (l), maximum width (w) and thickness (th) of 6 pedicle valves of *Serratocrista fistulosa* sp. n.

TABLE 13

$\bar{l}$ mm. (var.) = 5·75 (12·22)
$\bar{w}$ mm. (var.) = 8·33 (23·551)
r = 0·988
a (var.) = 1·389 (0·0058)

TABLE 13. Statistics of length (l) and width (w) of 10 brachial valves of *Serratocrista fistulosa* sp. n.

Family **MEEKELLIDAE** Stehli 1954

Subfamily **MEEKELLINAE** Stehli 1954

[= Omboniinae Sokolskaja 1960]

Genus ***SCHELLWIENELLA*** Thomas 1910

TYPE SPECIES. *Spirifera crenistria* Phillips 1836, by original designation of Thomas (1910 : 92).

Schellwienella radialis (Phillips)

(Pl. 6, figs. 13–24. Text-figs. 27–35)

1836 *Spirifera radialis* Phillips: 220, pl. 11, fig. 5.
1861 *Streptorhynchus crenistria* var. *radialis* (Phillips) Davidson: 129, pl. 25, figs. 16, 17, 18.
1930 ?*Schellwienella* aff. *aspis* Smyth: 555, pl. 16, figs. 6a, 6b.
1934 ?*Schellwienella aspis* var. *radialiformis* Demanet: 85, pl. 7, figs. 6–12.

DIAGNOSIS (emended). Dorsibiconvex to slightly resupinate *Schellwienella* with strong parvicostellate ribbing, strong divergent dental plates, small complete chilidium, high cardinal process and deeply impressed dendritic dorsal adductor scars in adult.

DESCRIPTION. Profile inequibiconvex, adult brachial valve strongly convex posteriorly, thickness about one-half shell width; shell length about three-quarters width, adult anterior margin commonly slightly uniplicate; ribbing unevenly parvicostellate, commonly with seven ribs per 2·5 mm., 5 mm. antero-medianly of dorsal umbo, costae consistently stronger than intercalated costellae; concentric lamellae, becoming crowded marginally; ventral interarea apsacline, pseudodeltidium arched, perideltidium indistinct; dorsal interarea short with chilidium of equal length; dental plates receding, diverging to floor of valve, posteriorly enclosing muscle field consisting of postero-medianly placed adductor scars flanked by pair of rounded triangular diductor scars; cardinal process prominent, wide and bilobed; socket plates at about 50° from hinge-line and curved to valve floor to enclose sockets; in adults ridges extend from socket plates to enclose oval dendritic adductor scars separated by slight median ridge; shell substance sparsely pseudopunctate.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Brachial valve (E.2054)	*c.* 30·0	*c.* 42·0
	Incomplete brachial valve (BB.52746)	*c.* 11·8	*c.* 15·4
	Complete brachial valve (BB.52747)	30·6	42·0
	Incomplete brachial valve (BB.52748)	*c.* 30·8	*c.* 40·0
	Crushed, incomplete shell (BB.52750)	*c.* 50·0	*c.* 59·0

TYPE LOCALITY AND HORIZON:

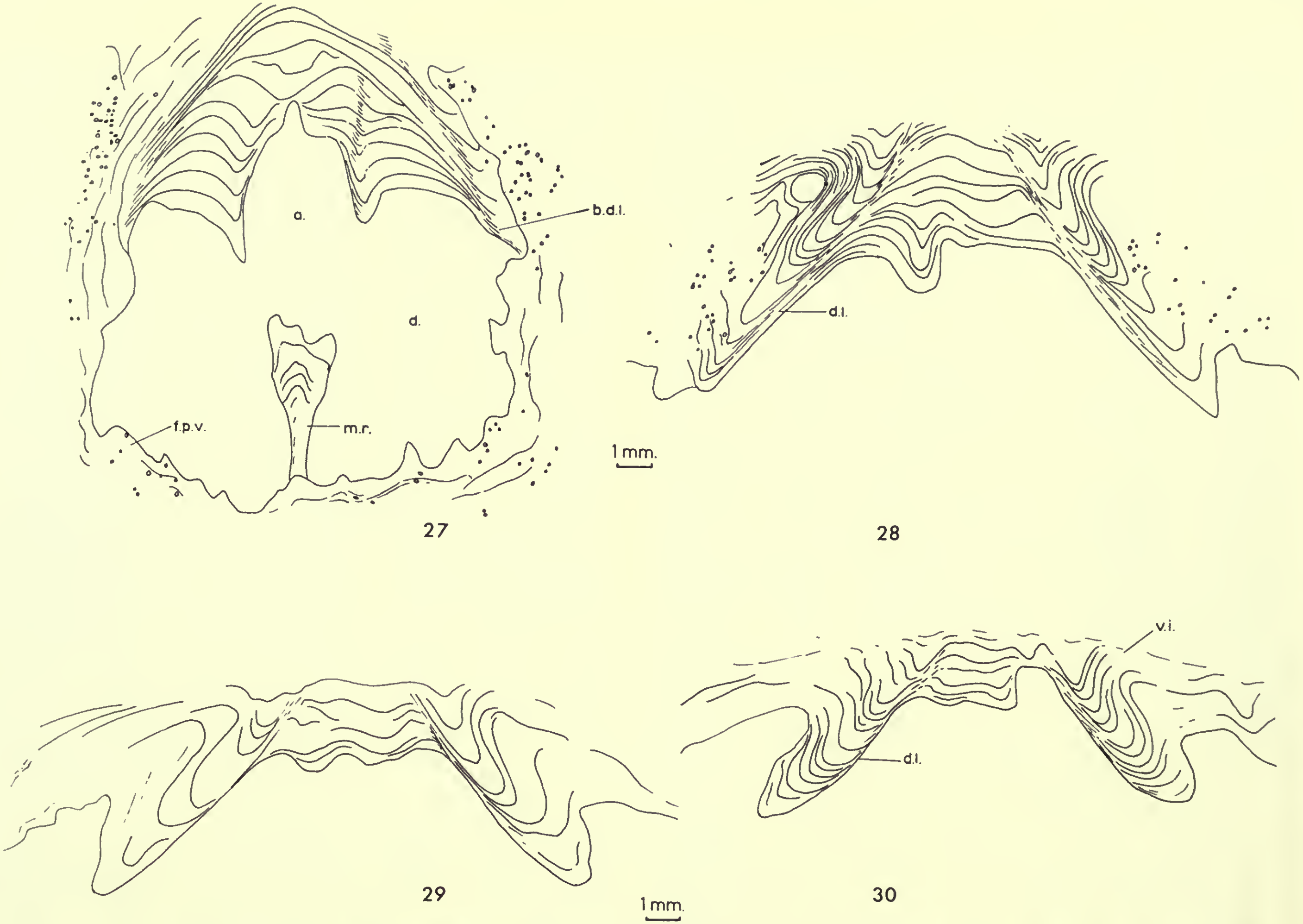
Holotype—in the University Museum, Oxford; No. E2054 collected by Phillips from the " Base of the upper Irish limestone " at Florence Court, about 12 miles S.E. of Derrygonnelly, Co. Fermanagh.

Other specimens from the argillaceous limestones and shales of Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh, or from underlying shale ½ mile upstream from Milltown Bridge, 1 mile N.W. of Church Hill, Co. Fermanagh. Low D. zone.

DISCUSSION. Although Thomas (1910 : 126) recorded the type material of *Spirifera radialis* Phillips as having been lost, the specimen figured by Phillips (1836, pl. 11, fig. 5) is actually preserved in the University Museum, Oxford, No. E.2054 and another specimen, No. E.2055, is possibly the second mentioned by Phillips on p. 220 as coming from Cumberland, but it is not as well preserved as the type specimen from Florence Court, Co. Fermanagh. Phillips described the Florence Court locality as being at the " Base of the Upper Irish limestone ", which is the lateral equivalent of the " reefal " limestones about 12 miles N.W., near Derrygonnelly, from below which the present material was collected. The lithology and fauna associated with the type specimen closely resembles the more shaly beds underlying the limestone horizon at Bunnahone from which the silicified fauna was collected. The type specimen itself shows only part of the dorsal exterior (Pl. 6, fig. 24), but in all known details it is closely comparable with the schellwienellas recovered from Bunnahone and for these reasons the horizons are considered comparable and the forms conspecific.

Thomas (1910 : 126) referred *Spirifera radialis*, " as ascribed by some British authors " to *Schuchertella*, a view followed by Demanet (1934 : 87) and Sarycheva & Sokolskaja (1952 : 43). One of Davidson's figures, (1861, pl. 25, fig. 17) however, clearly shows schellwienellid dental plates in an illustration of *Streptorhynchus crenistria*, var. *radialis* from Gare, Lanarkshire, and it is probable that all three figures, viz. 16, 17 and 18, are of *Schellwienella radialis*. Short, but well developed dental plates are clearly visible in the Fermanagh specimens . (Text-figs. 27–30, Pl. 6, fig. 17)

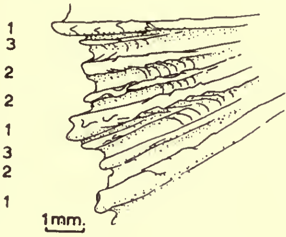
The differentiation between costae and intercalated costellae is clear in shells longer than 5 mm. The ribs are adorned by short dart-like projections, usually arranged alternately, one on either side of the rib crest, with a modal frequency of 3 per mm. between 4 and 5 mm. from the umbo. There is no clear correspondence between these serrations and the growth-lines, but the latter do project forward in crossing each rib, showing that growth was more rapid in this region (Pl. 6, fig. 19). In order to have maintained a more or less equally developed anterior margin, without greatly extended ribs, the mantle must have retracted more strongly at the rib crests than between them where shell deposition would have continued more evenly. This retraction of the mantle probably resulted in the formation of the spinose serration. The ornament contrasts with the undifferentiated ribbing arrangement of *Schellwienella aspis* Smyth, from Hook Head, Co. Wexford, in rocks of K, Z and C age. Smyth (1930 : 555), however, says that there is a tendency for



FIGS. 27-30. Illustrations of sections parallel to the commissural plane of the vertral umbonal region of *Schellwienella radialis* (Phillips). Pseudopunctate inner shell material surrounds the central space within which the ventral muscle bases were accommodated. The dental plates can be seen to fuse with the floor of the pedicle valve. *a*, adductor muscle region; *b.d.l*, base of dental plate; *f.p.v*, floor of pedicle valve; *m.r*, median ridge separating the paired muscle scars; *v.i*, ventral interarea.

the costae of specimens from the strata of C age to be stronger and for " . . . every fourth one to be emphasized ". Thus, it is possible that the ornamentation became more differentiated through strata of C and S age to that seen on *S. radialis* in Upper S and D strata.

The chilidium is well formed and in a brachial valve 11 mm. long was 2·7 mm. wide and 0·3 mm. long (Text-fig. 32) arching over the posterior face of the cardinal process in a postero-dorsal direction. A rudimentary chilidium can be distinguished



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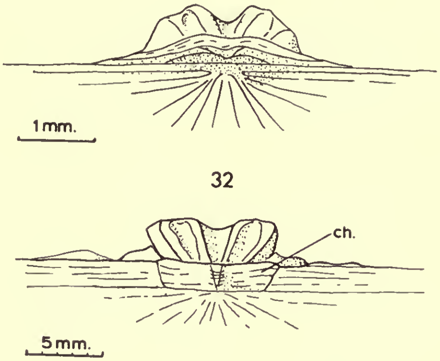

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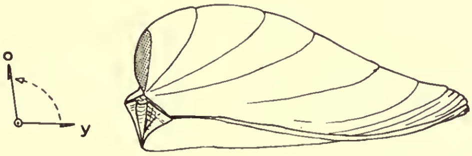

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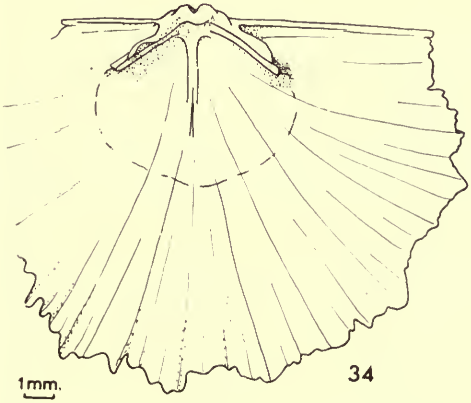

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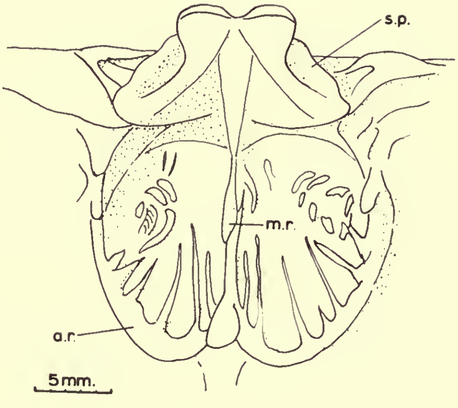

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FIGS. 31-35. Illustrations of *Schellwienella radialis* (Phillips) showing the morphology of the external radial ornamentation, (Fig. 31); the chilidium of young and adult specimens (Fig. 32); a lateral view of an adult shell and the rotation of the juvenile portion of the shell (stippled) relative to the hinge line (Fig. 33); and the cardinalia, viewed dorsally, in young (Fig. 34) and adult (Fig. 35) specimens. 1, costae; 2, first order costellae; 3, second order costellae; *a.r*, ridge surrounding the adductor scars; *ch*, chilidium; *m.r*, median ridge; *s.p*, socket plate.

in valves only 2·5 mm. wide, as bulbous projections postero-laterally of the cardinal process lobes, similar to those seen in *Brochocarina wexfordensis*. During growth the distal edge of the chilidium became directed posteriorly and finally ventrally. This resulted not so much from a differential growth of the chilidium itself but by the progressive rotation of the dorsal hinge-line resulting from increasing valve convexity (Text-fig. 33), and the considerable thickness of secondary shell at the anterior margins of gerontic valves. This angle of rotation may exceed 90° and in a specimen 52 mm. long approaches 110°. The cardinalia is typically davidsoniacean in young shells (Text-fig. 34) but became considerably thickened in old age. In adult shells the anterior face of the cardinal process became thickened so as to extend beyond the youthful socket plates, leaving a distinct groove between the two. The socket plates extend antero-laterally from the hinge-line at about 45° to 55° enclosing the sockets medianly. Although the bases of the socket plates curve to the valve floor to bound the sockets antero-dorsally, they do not recurve towards the hinge-line as in Orthotetinae. In shells more than about 40 mm. wide shell deposition formed ridges which extended from the socket plates around the adductor field. Postero-laterally within each adductor scar is an oval area, about one-third as long as the complete scar, which has a differentiated ornamentation and may have been the scars of posterior adductor muscles (Pl. 6, fig. 22).

In comparing the socket plates of different davidsoniacean subfamilies it must be recognized that while those of the Meekellinae are described as prolonged, as are those of the Streptorhynchinae and Derbyiinae, they do curve to the valve floor in a manner similar to the Schuchertellinae. However, the socket plates of the Schuchertellinae diverge from the hinge-line at a narrower angle than do those of the Meekellinae, while in the Orthotetinae they recurve towards the hinge-line with little anterior fusion to the valve floor.

Superfamily **CHONETACEA** Bronn 1862

The chonetacids are not considered to be a separate suborder, but to be sufficiently closely related to the Productacea to belong to the suborder Productidina. Muir-Wood (1962) discussed the classification of the chonetacids and followed her earlier works of 1955, and with Cooper 1960, by separating them from the Productacea in the belief that productaceans never had a functional pedicle. This has been shown to be incorrect (Brunton 1965) and at least some genera of both groups had functional pedicles during their earliest stages of ontogeny. A pedicle sheath was previously unrecorded from chonetacids above the Devonian but is now described in Fermanagh rugosochonetids and globosochonetids of Visean age.

It seems probable that Sarycheva & Sokolskaja (1959) are correct in uniting the Chonetacea and Productacea and their revertion to the previously held view that the Productacea were derived from the Chonetacea warrants careful consideration. The two groups are united by a comparable gross morphology, pseudopunctation and spine development and also by a similar phylogenetic trend to gigantism in the Lower Carboniferous. This may indicate a response to certain conditions by groups of organisms having arisen from the same ancestral gene pool. Probably during the

Devonian period the Productacea and Strophalosiacea differentiated from a chonetacean-like stock and rapidly diversified.

The plectambonitaceans possibly provided the ancestral stock from which the chonetacids arose, possibly late in the Ordovician. Some of the earliest strophochonetids, from Anticosti Island, Canada, are from beds commonly correlated with the Upper Llandovery or Lower Wenlock. *Eochonetes advena* Reed, described from the Upper Ordovician, Drummuck Group of Girvan, is plectambonitid in character but had hollow canals, passing from the interior towards the exterior of the posterior margin, which closely resemble the canals leading to the spines of Chonetacea. It is not known whether the canals of *Eochonetes* extended to the outer surface, and spines are unknown. But it is no great evolutionary step for the epithelial processes, or evanginations, already present in *Eochonetes* to have remained generative at their tips and to have grown posteriorly, accompanied by the deposition of shell so as to have formed spines.

Rib apertures have been observed and figured from the time of Davidson's monograph (1861) to Muir-Wood's recent chonetoid monograph (1962) in which she follows Dunbar & Condra (1932) in assuming that they are the bases of minute hollow spines. Muir-Wood (1962, pl. 6, fig. 6) illustrates the impression of the pedicle valve of a rugosochonetid which is said to show " spinules ". However, inspection of the specimen (BB.20424) shows that fragments of shell adhere to the mould from which taleolae or endospines protrude. Besides these there are fine obliquely disposed ridges of sediment aligned along the rib impressions. These are the sedimentary infillings of the rib apertures (" spinule bases "), but neither they nor the taleolae are " spinules " protruding from the outer shell surface. A similar phenomenon has been recorded by Demanet (1934 : 52) on moulds of *Schizophoria*, where infillings of the punctae by iron oxides have left a minutely spinose surface. On no specimens, either from Fermanagh or those studied by Davidson (1884, pl. 20, fig. 21), have actual " spinules " been observed and it seems more likely that a rib aperture was never the base of a true spine. The formation of the apertures probably took place by the sporadic inward sag of the mantle edge from the shell surface, and the resulting oblique hollows became sealed at their inner ends by the deposition of secondary shell. Anterior to each aperture, as growth continued, the rib regained its shape by the reversion of the mantle edge to its normal folded condition.

The morphology of the chonetacid hinge spines has attracted attention and it is generally agreed that their formation was as described by Williams (1956 : 252). However, Muir-Wood (1962 : 5) considers that chonetid spines differ from productacid spines in that the latter were open at their distal end. Evidence in support of this inference is lacking and it seems more reasonable, since the spines of both groups were capable of growth, that the distal ends were sealed by the generative tip of epithelium, covered by periostracum. The angle of emergence of the spines from the hinge-line varied during the growth of the shell and they commonly curved so that the distal part of the spine was at a different angle from that at which it arose from the posterior margin. The early formed, more medianly placed spines, tend to have a higher angle to the hinge-line than have those towards the lateral extremities. A feature of spine orientation, noted on the Fermanagh shells, is that the spines commonly extended posteriorly at the time of their origin. As a result of valve curvature, and consequent rotation of the shell relative to the substratum, the spines did not all grow parallel to the adult commissural plane. Thus, on adult shells the median spines may be dorsally directed while those towards the lateral extremities are progressively more posteriorly directed. This pattern of spine growth probably assisted in the stabilization of the shells on the substratum throughout life and after the pedicle had ceased to be functional.

Superfamily **CHONETACEA** Bronn 1862 *nom transl.* Shrock & Twenhofel 1953

Family **CHONETIDAE** Bronn 1862

Subfamily **ANOPLIINAE** Muir-Wood 1962

Genus ***GLOBOSOCHONETES*** nov.

Diagnosis. Small, strongly concavo-convex Anopliinae with strong ribbing and pair of ventrally serrated, anteriorly divergent septa in brachial valve.

Description. Shell small, outline semi-elliptical with rounded prominent umbo, hinge-line widest part of shell; profile highly concavo-convex, medianly arched, adult shells with four pairs of spines at high angle to hinge; young furnished with pedicle sheath; multicostellate, commonly comprising sixteen costae branching dichotomously or with rarely intercalated costellae, ribs rounded and more prominent on pedicle valve; ventral interarea orthocline, narrow with open delthyrium and indistinct arched apical pseudodeltidium, dorsal interarea rarely developed; teeth short and poorly differentiated from ventral interarea; median septum high, posteriorly confined but commonly extended anteriorly as low ridge for about one-third valve length; radially arranged tubercles correspond to external intercostal spaces; cardinal process undifferentiated internally, externally with V-shaped myophore laterally supported by elongate, low socket ridges, almost parallel to hinge-line; short lateral septa variable developed; pair of high septa cross dorsal visceral disc almost to anterior margin, at about 12° from mid-line; adductor scars indistinct, divided by lateral septa; radially tuberculate as dorsal valve; shell pseudopunctate.

Type species. *Globosochonetes parseptus* sp. n.

Discussion. The small size of these shells, together with their great convexity and pair of prominent plate-like accessory septa across the dorsal interior, are features common to genera included by Muir-Wood (1962) in her subfamily Anopliinae. Although these genera are all described as having smooth shells, save for growth lines, she does appear to allow for costellation in her subfamilial diagnosis by saying "shell normally smooth", (1962 : 32). Thus the new genus, *Globosochonetes*, is here included within the Anopliinae and differs from *Anoplia*, *Anopliopsis*, *Chonetina*, *Notanoplia* and *Tornquistia* in being strongly ribbed. The ribbing and arrangement of internal tubercles is intimate, so that while the latter are more or less scattered within smooth genera, they are radially arranged in *Globosochonetes*. The genus differs from *Plicochonetes*, of the Rugosochonetinae, with which it may have been confused in the past, by its poorly differentiated cardinal process, strong dorsal septa, finer ribbing and smaller size.

Globosochonetes parseptus gen. et sp. n.

(Pl. 7, figs. 8–27, Text-figs. 36–41)

DIAGNOSIS. As for genus.

DESCRIPTION. Small, deeply convex shells, one-third as deep as wide, four-fifths as long as wide, with narrow body cavity; ventral umbo of young shells flattened or grooved, provided with supra-apical pedicle sheath; costation rounded, even and prominent except on umbones, costellae commonly dichotomously branched within first 2 mm. of ventral beak; five ribs occur in 1 mm. width, 2 mm. antero-medianly from ventral umbo; adult hinge-spines slightly recurved towards mid-line, increasing in size laterally, ventral median septum prominent and thickened in beak adjacent to cardinal process; adductor scars oval, posteriorly placed, flanked by anteriorly spreading diductor scars; poorly differentiated cardinal process with small alveolus bordered by median ends of socket ridges that extend about one-half valve width and enclose shallow sockets; lateral septa indistinct, at about 45° to hinge-line and separate poorly defined posterior adductor scars from anterior adductor scars; pair of high accessory septa diverge from mid-line at 10° to 15°, serrated distal edges commonly exaggerated in geronitc shells; small, posteriorly placed, lobate median septum developed late in life.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52751)	3·1	4·1
PARATYPES.	Complete pedicle valve (BB.52752)	3·5	4·8
	Incomplete brachial valve (BB.52753)	2·7	—
	Complete brachial valve (BB.52755)	1·3	1·6
	Incomplete pedicle valve with pedicle sheath. (BB.52756)	—	3·5
	Incomplete pedicle valve with pedicle sheath. (BB.52757)	—	1·7
	Incomplete brachial valve (BB.52754)	—	3·9
	Complete shell (BB.55498)	3·7	4·4
	Brachial valve (BB.55499)	*c.* 1·9	*c.* 2·6
	Incomplete shell (BB.55783)	3·1	3·6

TYPE LOCALITY. Sillees River, about 300 yds. east of Bunnahone Lough (low D zone).

DISCUSSION. Two small specimens in the Davidson Collection of the British Museum (Nat. Hist.) (B.14174) from Settle, Yorkshire, which are possibly the originals for figure 18, plate 47 of Davidson (1861), are externally indistinguishable from the Fermanagh shells. Both have the same shape and rib counts. Although the interiors of the Davidson specimens are not known, they are thought to be conspecific with *G. parseptus*.

The Fermanagh species is apparently similar to *Chonetes minuta* Goldfussi *sensu* de Koninck (1847 : 219, pl. 20) from the Devonian Eifel region. However, *C. minuta* is longer (length is given as 12 mm. by de Koninck) and the ribbing apparently more coarse, i.e. 22 ribs in all. *G. parseptus* is comparable in size and shape to *Leptaena* (*Chonetes*) *subminima* M'Coy. However, inspection of the type specimens from the Sedgwick Museum, Cambridge (E.6773–6780) shows that M'Coy's species has a finer costellation, viz. about 14 ribs per one mm., 1 mm. antero-medianly from the ventral umbo (cf. Table 14). The poorly preserved dorsal interior shows no sign of the strong septa present in the Fermanagh species and the two are not conspecific. Neither is M'Coy's material conspecific with the specimen " from the Namurian of the river Hodder, Yorkshire " (B.53889) which Muir-Wood (1962 : 62) tentatively identified as " *Chonetes* [?*Plicochonetes*] *subminimus* (McCoy) ". The Hodder specimen has a rib count similar to that of *G. parseptus* and the two could be congeneric.

Tornquistia polita (M'Coy) resembles the new species in size, shape and dorsal interior but differs in being devoid of all ribbing.

Muir-Wood (1962 : 6) speaks of the young of some Devonian and Silurian chonetids having been attached by a pedicle which emerged through the ventral umbo and formed a " small pedicle pipe ". The present Visean chonetids are probably the first of this age to be recorded showing the structure, here called the pedicle sheath. It was almost certainly not functional in valves 3 mm. long because the ventral beak of such valves is filled by secondary shell at the posterior end of the median septum. With a maximum diameter of only about 0·03 mm., it is unlikely that the pedicle was functional for long after the spat had settled, or that its growth continued beyond the neanic stage: certainly no internal opening has yet been distinguished in valves longer than 1·2 mm. The pedicle sheath is essentially the same structure as is seen in several genera of the productacea, and it does seem that a functional pedicle was more common in the early stages of brachiopod development than is often supposed. Unlike Muir-Wood (1962 : 6) the writer considers the pedicle sheath to be a feature of both strophomenoids and productoids, and one which indicates the close relationship of the two groups.

During growth, the rate of shell deposition appears to have been greatest on the flanks, so that the pedicle valve became highly arched medianly and in these regions occurred the greatest proliferation of the costae. In some shells this pattern of growth led to a slight flattening of the antero-median venter. Costae are absent from the first 0·5 mm. of the shell and less prominent upon the brachial valve. 2, 6, 12, 1 and 1 specimens have respectively 14, 15, 16, 17 and 18 costae. Branching most commonly occurred within the first 1·5 mm. from the pedicle beak and was usually of a dichotomous nature, especially on the pedicle valve. However, about three-fifths of the costellae of both valves were added by external, (i.e. lateral) branching or by intercalation, and any one specimen may show all these types of rib addition.

Of the four pairs of hinge-spines, the last formed are the largest, and although they arose from the hinge-line at an angle of about 120°, they soon curved inwards to become parallel or even convergent to the mid-line. As would be expected, the spines arose at regular intervals, the third and fourth at valve lengths of about 2 and 3 mm. respectively. The means (with variances) of the distances between the spines are given in Table 15.

The first pair of spines were of very small diameter, like the pedicle sheath, and were soon internally sealed. The second pair remain open in valves about 1·2 mm. long, but beyond this size soon became closed by the antero-lateral growth of the interarea and teeth. The third and fourth pairs of spines commonly retain their internal connections, opening anterior of the interarea (Pl. 7, fig. 14). The teeth are commonly indistinctly differentiated from the interarea by a slight ridge, although in some specimens they are more distinct and diverge from the hinge-line at an angle of up to 10°.

The ventral median septum is distinguishable in valves 1·2 mm. long, and arose from the beak (Text-fig. 37). At this growth stage the adductor scars from a subrounded, rather flat area within the ventral umbo. Beyond this stage convexity was such as to reorientate the muscle field from being dorsally to anteriorly directed and within these adult shells the adductor field is divided by the septum, which, while remaining confined to the umbonal region, is extended anteriorly as a low ridge for nearly one-third the length of the valve (measured parallel to the commissural plane).

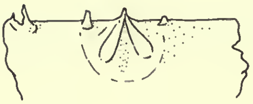
The protegulal node is well seen on brachial valves, having been protected from abrasion by the shell convexity. It is commonly 0·3 mm. in length and about one-half the width, and is represented internally by the alveolus, lying between the cardinal process base, the socket ridges and the posterior ends of the strong accessory septa, which are 0·15 mm. apart (Text-fig. 40). The septa are highest at about mid-valve length and always have serrated distal margins, the serrations being anteriorly directed and lobate in herontic shells (Text-fig. 41). These septa were probably supporting structures to the brachial apparatus and within these small shells may have assisted in the separation of the water currents in the brachial cavity.

A short median septum can be distinguished in dorsal valves of about 2 mm. in length. It continued to grow by secondary shell accretion over the median row of tubercles so that in valves about 3 mm. long it extended nearly 1 mm. anteriorly of the hinge-line. The alveolus always remained free of secondary structures (Pl. 7, figs. 21, 26).

TABLE 14

Ribs	4	5	6	7
A	0	23	41	10
B	8	21	6	0

TABLE 14. The number of ribs counted in a width of 1 mm. at 1 mm. (A) and 2 mm. (B) antero-medianly of the ventral umbo of *Globosochonetes parseptus* gen. et sp. n.



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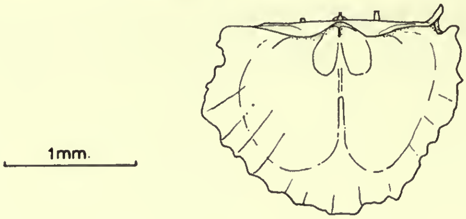

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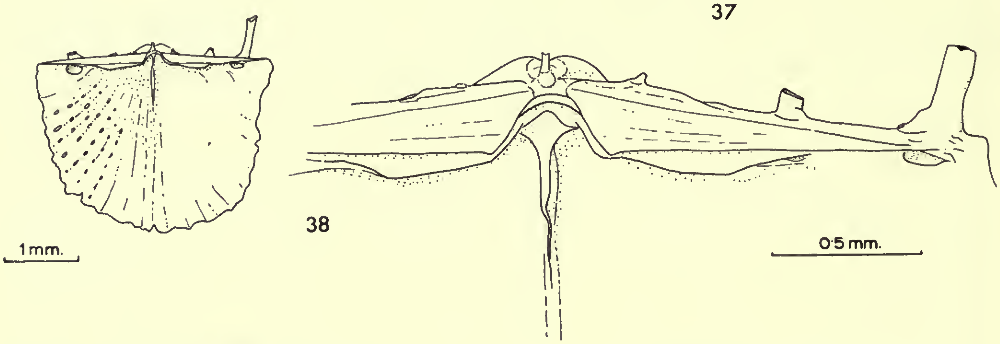

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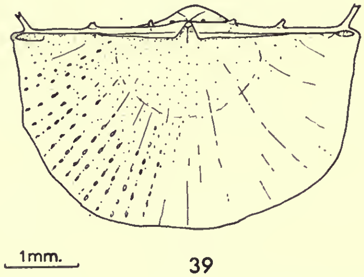

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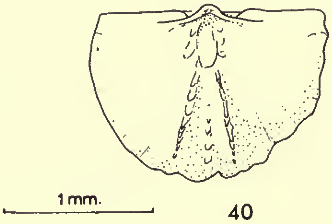

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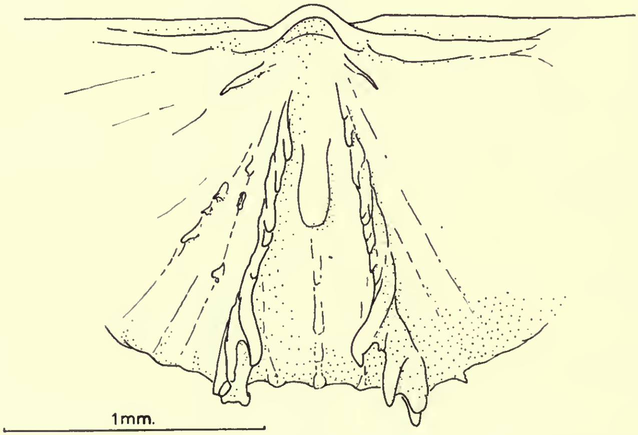

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Figs. 36-39. Illustrations of the ontogeny of the pedicle valve of *Globosochonetes parseptus* gen. et sp. n., Fig 36 is the external view of the same specimen as Fig. 37 within which muscle scars, probably adductors, are clearly developed.

Figs. 40-41. Brachial valve interiors of young and adult specimens of *G. parseptus*. The depression anterior to the cardinal process of the young valve is represented externally by the protegular node.

TABLE 15

	Between umbo and 1st	Between 1st and 2nd	Between 2nd and 3rd	Between 3rd and 4th	Between outer spines	Valve length
Mean (mm.)	0·28	0·40	0·60	0·74	2·66	2·66
(var.)	(0·0017)	(0·00069)	(0·0065)	(0·0125)	(0·190)	(0·266)
n.	30	30	27	5	30	30

TABLE 15. Statistics of the distances between hinge-spines (numbered outwards from the umbo) of *Globosochonetes parseptus* gen. et sp. n., together with the total distance between the outer pair of spines and the length of the valves.

TABLE 16

$\bar{l}$ mm. (var.) = 2·15 (0·266)
r = 0·946

$\bar{w}$ mm. (var.) = 2·61 (0·960)
a (var.) = 1·315 (0·00371)

TABLE 16. Statistics of length (l) and maximum width (w) of 51 pedicle valves of *Globosochonetes parseptus* gen. et sp. n.

TABLE 17

$\bar{l}$ mm. (var.) = 2·30 (0·272)
$\bar{w}$ mm. (var.) = 2·89 (0·370)
r = 0·959
a (var.) = 1·171 (0·00427)

$\bar{l}$ mm. (var.) = 2·30 (0·272)
$\overline{th}$ mm. (var.) = 0·99 (0·060)
r = 0·895
a (var.) = 0·469 (000169)

TABLE 17. Statistics of length (l), maximum width (w) and thickness (th) of 28 shells of *Globosochonetes parseptus* gen. et. sp. n.

TABLE 18

$\bar{l}$ mm. (var.) = 1·98 (0·216)
r = 0·729

$\bar{s}$ mm. (var.) = 0·52 (0·0147)
a (var.) = 0·263 (0·00088)

TABLE 18. Statistics of valve length (l) and the distance between the anterior ends of the accessory septa (s) of 39 brachial valves of *Globosochonetes parseptus* gen. sp. n.

Subfamily **RUGOSOCHONETINAE** Muir-Wood 1962

Genus ***RUGOSOCHONETES*** Sokolskaja 1950

TYPE SPECIES. *Orthis hardrensis* Phillips 1841, pars, by original designation of Sokolskaja (1950 : 23).

DISCUSSION. Diagnosis of the genus depends upon an understanding of *R. hardensis*. The species was discussed by Muir-Wood (1962) who selected a lectotype from amongst the Phillips specimens from Hardraw, Wensleydale, now at the University Museum, Oxford, (E.1571). Neither this specimen nor the remaining Hardraw specimens at Oxford are particularly well preserved, being moulds or somewhat crushed specimens in shale. The lectotype, and two other specimens (E.1577, 1578), show distinct lobate areas on either side of the mid-line presumably accentuated by sediment compaction and slight crushing of the shell. These areas exactly match elevated regions seen on the dorsal interior of a specimen from Ray Gill, near Hawes, Wensleydale (Geol. Surv. Mus. 95131), which are assumed to mark the regions enclosed by the spirolophe. Further collecting is required to ascertain whether this dorsal morphology is a consistent and specific feature. The similarly sized specimens E.1569 (Univ. Mus. Oxford) and BB.41147 (British Museum (Nat. Hist.)), figured by Muir-Wood (1962), show dorsal interiors without distinguishable brachial areas and such specimens may prove to be distinctive.

In comparing the Fermanagh rugosochonetids with the types of *R. celticus* it became apparent that the specimens assigned by Muir-Wood to this species belong to three distinct groups. The holotype (BB.41145) from Flintshire, North Wales, (Pl. 7, figs. 28–31) together with other specimens from Flintshire and elsewhere in Britain are distinguishable by their clear and fine ribs. Five, 25 and 8 specimens have respectively 4, 5 and 6 ribs per mm. at 4 mm. from the ventral umbo. Muir-Wood (1962 : 69) mentions a coarsely ribbed variant and these valves were figured as being conspecific. Three, 10 and 4 specimens have respectively 2, 3 and 4 ribs per mm. at 4 mm. from the ventral umbo (e.g. B.53892 and 68475 in Brit. Mus. (Nat. Hist.) (Pl. 8, figs. 2–5), and although they have been found at the same localities as the fine ribbed *R. celticus* s.s., appear to have other distinctive features. The coarse ribbed shells have more prominent rib apertures and a relatively longer ventral median septum than have the finely ribbed group, and the ventral adductor scars are distinctive in being slightly raised above the floor of the valve.

The *R. celticus* picture is further complicated by specimens from Northumberland and Fifeshire which are poorly ribbed (e.g. B.42046, BB.41100–01 and B.53929–34) (Pl. 8, figs. 6–9). While the rib frequency is consistent with *R. celticus* s.s., the ribbing is absent postero-laterally, near the posterior margin, and commonly replaced anteriorly, after a valve length of 7–9 mm., by irregular but prominent " growth-lines ". This anterior region is commonly infested by boring organisms and it may be that an ecological factor effected the growth of these shells. They further differ by their slightly greater width, relative to length; flatter umbo and smoother ventral diductor scars than in *R. celticus* s.s. Owing to the poorly developed ribbing, the internal valve margins are not strongly crenulated.

The distinctions between *R. celticus* and *R. hardrensis* are slight. Muir-Wood (1962 : 70) says that the former is larger, more convex in profile, has spines extending from the hinge at a lower angle, and " has slight internal differences " from *R. hardrensis*. The few complete shells assigned to *R. hardrensis* from the Hardraw or Gayle shales of Wensleydale that are available for study (Geol. Surv. Mus. 93151–93152; Brit. Mus. (Nat. Hist.) B.80965–80966, and BB.52661–52666) are almost indistinguishable from the holotype of *R. celticus*. One Wensleydale specimen in the Geological Survey Museum (93152) is 0·5 mm. longer and wider than the holotype of *R. celticus* and differs in shape by being almost 20 % thicker! The rib frequency is 25 in 5 mm. at 5 mm. from the ventral umbo in both specimens. The difficulty in comparison lies in the poor preservation of the *R. hardrensis* lectotype and in deciding if this specimen is conspecific with the *R. celticus*-like Wensleydale specimens. If this were so *R. celticus* would be a junior synonym of *R. hardrensis.* However, until a large localised collection can be studied to enable valid comparisons to be made, the two species must remain. Within *R. celticus* Muir-Wood distinction should be drawn between the finely ribbed holotype group; the coarsely ribbed group and those with poorly developed ribbing. These groups may well warrant at least subspecific designation.

Rugosochonetes silleesi sp.n.

(Pl. 8, figs. 10–27; Text-figs. 42–50)

DIAGNOSIS. *Rugosochonetes* with strongly convex pedicle valve and prominent umbo; multicostellate with 6 ribs per mm., 4 mm. from dorsal umbo, rib apertures present.

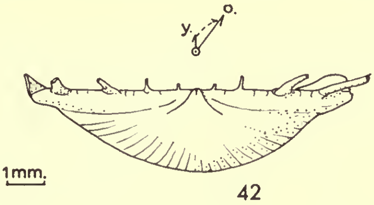
DESCRIPTION. Outline semielliptical with length about two-thirds maximum width, hinge-line straight; shell unequiconcavo-convex with rounded ventral umbo extending beyond hinge-line, thickness approximately one-third hinge width; hinge spines extend posteriorly at about 30° to median plane, seven pairs on adult valves; multicostellate, ribs rounded, as wide as interspaces; about twenty-five costae, costellae commonly added by intercalation on brachial valve and by dichotomy on pedicle valve; about six ribs per 1 mm. width, 4 mm. antero-medianly of dorsal umbo, rib apertures sparsely developed; fine concentric growth-lines indistinct; ventral interarea anacline to orthocline, short, delthyrium quadrate to triangular, pseudodeltidium apical, much reduced; dorsal interarea hypercline, reduced, small chilidial plates flank notothyrium; teeth set slightly below and parallel to plane of interarea, grooved on ventral surfaces; median septum high umbonally, thickened below delthyrial apex, in adult shells extending one-third valve length as low ridge; ventral muscle field flabellate, adductor scars pear-shaped, diductor scars elongately triangular, bounded postero-laterally by distinct shell thickening; hinge spines commonly communicating internally through oblique canals; cardinal process bilobed, poorly differentiated, myophores dorsally directed, V-shaped and incised; cardinal process laterally supported by socket ridges at about 20° to hinge-line, which enclose well defined sockets anteriorly; alveolus well defined; median septum extends about one-half length of adult valve; lateral septa prominent anteriorly, disposed at 30° to mid-line, and extending for about one-third length of adult valve; dorsal muscle field indistinct, posterior and anterior adductor scars pear-shaped and oval, separated by posterior ends of lateral septa; both valves internally ornamented by anteriorly directed radial rows of tubercles corresponding to external interspaces and pseudo-punctation, valve margins internally ribbed.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52758)	9·6	12·6
PARATYPES.	Complete pedicle valve (BB.52759)	9·6	12·7
	Incomplete pedicle valve (BB.52760)	—	13·0
	Complete brachial valve (BB.52761)	9·1	14·4
	Incomplete brachial valve (BB.52762)	10·3	—
	Complete brachial valve (BB.52763)	2·8	3·9
	Complete brachial valve (BB.52764)	7·7	11·8
	Complete shell (BB.52766)	9·8	13·0
	Complete pedicle valve (BB.52765)	7·0	8·9
	Incomplete pedicle valve (BB.52767)	3·7	c. 4·9
	Complete shell with pedicle sheath (BB.52768)	1·6	2·0
	Shell crushed in shale (BB.52769)	c. 11·1	c. 17·2
	Shell crushed in shale (BB.55784)	c. 11·0	c. 17·2
	Incomplete shell (BB.52770)	4·7	—

TYPE LOCALITY. Sillees River, about 300 yds. east of Bunnahone Lough (low D zone)

DISCUSSION. The Fermanagh material is in general accordance with several features described or illustrated by Muir-Wood for *R. celticus* (1962 : 68). However, the shells only rarely reach the dimensions given by her, " about 19 mm. wide, 14 mm. long, and 3 mm. thick ", in the shales below the silicified limestone horizon which yields the present sample. More important distinctions are in the proportions of size and ribbing. Selecting 38 shells of *R. celticus* s.s. (i.e. holotype and conspecific specimens with the fine ribbing taken from a number of localities, in the British Museum (Nat. Hist.) collections) 5, 25 and 8 specimens have respectively 4, 5 and 6 ribs per 1 mm. width, 4 mm. antero-medianly. This compares with 6, 20 and 3 specimens of *R. silleesi* having respectively 5, 6 and 7 ribs per mm. (Table 21). The thickness of the shell, compared to length, is consistently greater in *R. silleesi* as a result of the deeper, more prominently rounded ventral umbo; the relative shell length is also slightly greater. The shell outline underwent little change during growth other than becoming relatively wider, although the cardinal extremities were usually obtuse and only rarely represented the widest part of the shell. This variability seems to have resulted from an acceleration of growth in a lateral direction during the formation of each pair of spines. The spines, which number seven pairs in adult shells, arose with fairly regular spacing along the posterior margin of the ventral interarea (Table 22). It is frequently impossible to distinguish the sites of the first formed spines, and for this reason measurements were always taken from the mid-line of the valve to the second pair of spines. However, when the first pair were distinguishable, measurements were made and range from 0·35 to 0·6 mm., with a modal value of 0·4 mm. The spines become stronger laterally, the sixth pair commonly being about 0·2 mm. in diameter. Most spines are inserted obliquely to the posterior margin of the valve but almost immediately continued to grow posteriorly at a high angle from the posterior margin of the valve. At each stage of growth the spines were posteriorly projecting so that in the adult shell the oldest, median spines, are nearly dorsally directed, while the youngest, lateral spines, project posteriorly (Text-fig. 42). This indicates the degree of rotation relative to the hinge-line during growth. Most commonly the spines retained hollow connection to the valve interior throughout adulthood (Pl. 8, fig. 22). The lateral two or three pairs of spines have broad direct openings to the interior, anteroventral of the hinge-line, while the median three or four pairs retain connection by obliquely disposed canals through the interarea, so as to open ventro-laterally of the teeth. In a shell 13·0 mm. wide along the hinge-line, the second and third pairs of spines have canals, 0·8 mm. long, running through the interarea at about 70° to the mid-line.



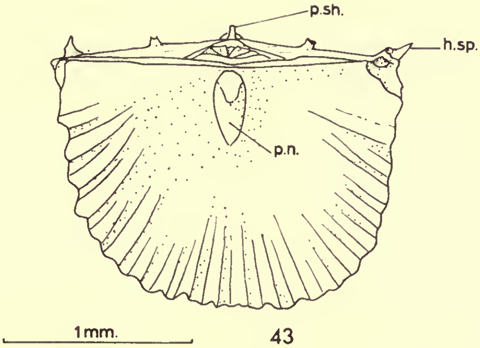


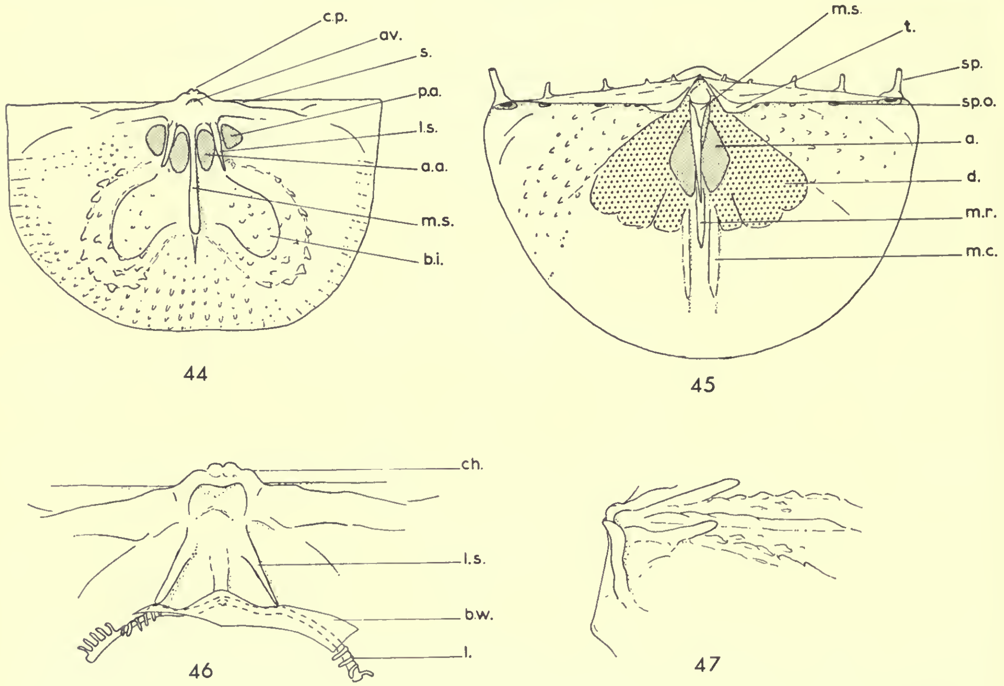
FIG. 42. Posterior view of a rugosochonetid shell showing the way in which rotation of the commissural plane relative to the horizontal led to a swing in the orientation of the hinge-spines from being dorsally directed, medianly, to posteriorly directed, laterally, in adult shells; *y* and *o* indicate the spine orientation relative to the hinge-line axis of the spines formed in youth and old-age respectively.

FIG. 43. Illustration of a young rugosochonetid shell viewed postero-dorsally; *h.sp*, hinge-spine; *p.n*, protegulal node; *p.sh*, pedicle sheath projecting from the tip of the ventral umbo. The cardinal process is bilobed and a rudimentary chilidium is commonly distinguishable.

The convexity of the pedicle valve is regular in the mid region, but there is flattening towards the cardinal extremities to form small ears. The brachial valve is flat for the first 1·0 mm., around the prominent protegulal node (Text-fig. 43).

Beyond this length concavity of the valve is gentle and regular so as to meet the pedicle valve towards the anterior margin as a short trail.

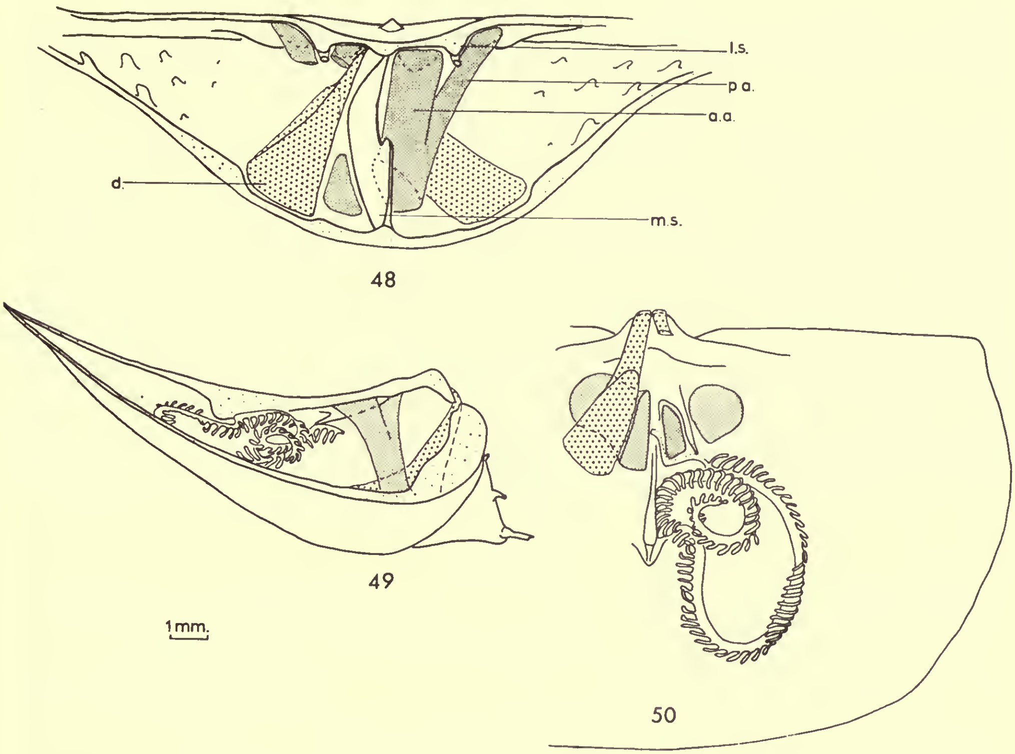
The radial ornament is equally conspicuous on both valves. although obscure for about the first 1 mm. of both valves. The ribs are prominent, rounded and of much the same wave-length as the interspaces, each one slightly increasing in size towards the anterior margin. Table 23 shows the range in the number of costae observed on brachial valves. The number counted on pedicle valves is consistently comparable, and within the same range fo four. On the brachial valve costellae are most commonly added by intercalation; this is almost invariably so over the median region of the valve, but on the flanks sporadic dichotomy of the ribs is usual. Intercalation is rare on the pedicle valves and dichotomy is the usual method of branching (Table 24). Thus the ribbing is complimentary and ventral dichotomy is usually accompanied by dorsal intercalation during growth. Muir-Wood (1962 : 9) wrote of the " elongate-trigonal perforations " seen on the ribs of " most chonetids ", as being



44 45 46 47

FIGS. 44-47. Illustrations of principal internal morphological features of chonetids; brachial valve (Fig. 44), pedicle valve (Fig. 45); a reconstruction of the postero-median segment of the sylized lophophore and body wall supported by the lateral septa (Fig. 46); and a lateral view of the lateral septa (Fig. 47), *a.a*, anterior adductor scar; *a*, ventral adductor scar; *av*, alveolus; *b.i.*, brachial impression; *b.w*, body wall; *ch*, chilidium; *c.p*, cardinal process; *d*, ventral diductor scar; *l*, stylized lophophore; *l.s*, lateral septum; *m.c*, trace of a mantle canal; *m.r*, median ridge; *m.s*, median septum; *p.a*, posterior adductor scar; *s*, socket; *sp*, spine; *sp.o*, internal spine opening; *t*, tooth.

the " base of small hollow spinules which were very fine and delicate and are rarely preserved in place ". These apertures are irregularly and sparsely distributed on the ribs of *R. silleesi* as anteriorly directed arches temporarily terminating the rib. Anteriorly the rib regained its normal dimensions over a distance of less than 0·5 mm. (Pl. 9, figs. 1, 2). The same sort of structure is to be seen on the ribs of *Schizophoria* and *Rhipidomella* from the same locality. The apertures were formed by the temporary retraction or sagging of the mantle edge from the inner shell surface of the rib so that deposition ceased to form a rib until the mantle had once again become folded. Muir-Wood has referred to the taxonomic importance of these " spinulus ". Certainly there seems to be a genetical control within brachiopods as a whole, governing the formation of these apertures; a control which is of systematic importance amongst Lower Palaeozoic orthaceans and enteletaceans.



Figs. 48-50. Stylized reconstructions of the musculature and inferred position of the diagrammatic lophophore in *Rugosochonetes silleesi* sp. n. as seen in transverse section from the anterior (Fig. 48), in longitudinal section (Fig. 49), and the brachial valve interior (Fig. 50), *a.a*, anterior adductor muscle; *d*, diductor muscle; *l.s*, lateral septum with its prolongation showing as a discrete position of shell between the dorsally divided adductor muscles; *m.s*, ventral median septum; *p.a*, posterior adductor muscle.

The ventral beak of young shells is grooved, in a similar way to that of *Globosochonetes*, but a pedicle sheath is only rarely preserved (Pl. 8, fig. 26). The median septum was developed from the earliest stages, but only in shells longer than about 5 mm. is the median ridge developed anteriorly of the high umbonal septum.

Within the dorsal valve, the lateral septa, or anderidia of Sadlick (1965 : 157) became prominent in valves more than 5 mm. long, prior to which the septa are little more than raised tuberculate regions with a posteriorly placed ridge of about 0·3 mm. In adult shells the septa developed anteriorly forming distinct prongs. From their anterior ends indistinct reniform areas, enclosed by a slight ridge or by tubercles, can be seen extending beyond the median septum for about two-thirds of the valve length (Text-fig. 44). The dorsal median septum is low and flattened, except anteriorly (Pl. 8, fig. 23). This flattening did not result from restriction within the body cavity of the shell as the valves are well separated in this region. The lateral septa (anderidia) are thought to have given support to the posterior ends of the primary loop of the spirolophe (Text-fig. 46), which was itself partly supported by the median septum and partly from the reniform markings antero-lateral of the median septum. Such an arrangement of the brachial apparatus would have been similar to that illustrated by Williams (1956) in fig. 5 (6) for *Productus* s.s. Text-figs 48–50 show the inferred gross anatomy of the species. If this interpretation is correct, the prolongations of the lateral septa (anderidia) protuded anteriorly of the visceral cavity, as defined anteriorly by the inferred paths of the adductor muscles. It is envisaged that the prolongations supported the anterior body wall at the points from which the lophophore was supported. Sadlick (1965 : 158) describes the anderidia as being in the coelomic cavity and well behind the body wall, and argues

TABLE 19

$\bar{l}$ mm. (var.) = 6·11 (8·7144)
$\bar{w}$ mm. (var.) = 8·02 (15·213)
r = 0·992
a (var.) = 1·321 (0·00073)

$\bar{l}$ mm. (var.) = 6·11 (8·7144)
$\overline{th}$ mm. (var.) = 2·29 (2·0567)
r = 0·920
a (var.) = 0·486 (0·00110

$\overline{th}$ mm. (var.) = 2·29 (2·0567)
$\bar{x}$ mm. (var.) = 7·08 (12·039)
r = 0·972
a (var.) = 2·419 (0·00847)

TABLE 19. Statistics of length (l), maximum width (w), thickness (th) and width of hinge-line (x) of 40 shells of *Rugosochonetes silleesi* sp. n.

TABLE 20

$\bar{l}$ mm. (var.) = 6·77 (1·422)
$\bar{s}$ mm. (var.) = 3·17 (0·739)
r = 0·959
a (var.) = 0·721 (0·00350)

TABLE 20. Statistics of length (l) and length of the median septum (s), measured from the hinge-line, of 14 brachial valves of *Rugosochonetes silleesi* sp. n.

TABLE 21

No. of ribs	5	6	7	8
At 2 mm. from umbo	1	11	16	2
At 4 mm. from umbo	6	20	3	0

TABLE 21. Ribs counted per 1 mm. width at distances of 2 mm. and 4 mm. anteromedianly from the dorsal umbo of *R. silleesi* sp. n.

TABLE 22

Distances between spines	Umbo and 2nd	2nd and 3rd	3rd and 4th	4th and 5th	5th and 6th	6th and 7th
Mean (mm.)	0·90	0·74	1·018	1·22	1·26	1·35
(Var.)	(0·01214)	(0·0182)	(0·0395)	(0·0157)	(0·0257)	
N	29	28	22	15	8	2

TABLE 22. Distribution of hinge-spines. Distances measured from the mid-line to the second spine and subsequently between additional spines of *R. silleesi* sp. n.

TABLE 23

No. of costae on dorsal valves	20–23	24–27	28–30
No. of specimens	4	18	6

TABLE 23. The number of costae counted on 28 dorsal valves of *Rugosochonetes silleesi* sp. n.

TABLE 24

<table>
<tr><th rowspan="2"></th><th colspan="3">Dichotomy</th><th rowspan="2">Intercalation</th></tr>
<tr><th>Flanks</th><th>Median sector</th><th>Both</th></tr>
<tr><td>Brachial valves</td><td>19</td><td>2</td><td>2</td><td>30</td></tr>
<tr><td>Pedicle valves</td><td colspan="3">30</td><td>4</td></tr>
</table>

TABLES 24. Scoring for the method by which costellae were added on 53 brachial valves and 34 pedicle valves of *R. silleesi* sp. n.

that they could not have been used for lophophore attachment. While this is agreed, nevertheless it is considered that these ridges developed functionally as posterior supports to the lophophore and that in life the anteriorly projecting processes were probably prominent in adult shells. Having restricted the anderidia to the coelomic cavity Sadlick can hardly suggest that " long anderidia undoubtedly helped form a channel for inhalent currents " (1965 : 158).

Rugosochonetes delicatus sp. n.

(Pl. 9, figs. 3–15, Text-figs 51, 52)

DIAGNOSIS. Gently concavo-convex *Rugosochonetes* with flattened ventral umbo, thin-shelled; finely and indistinctly multicostellate with few rib apertures; muscle scars obscurely developed.

DESCRIPTION. Outline subsemicircular, about two-thirds as long as wide, greatest width at straight hinge-line with poorly defined triangular ears; profile concavo-convex, pedicle valve evenly convex, umbo flattened, not extending beyond hinge-line, thickness one-quarter to one-third length, body cavity narrow; adult shells with four pairs of hinge-spines at 30° to 40° from mid-line; multicostellate, ribs low and rounded, umbones smooth, costellae rarely added by dichotomy and intercalation, commonly 7 ribs per mm. width, 2 mm. or 4 mm. anteromedianly of pedicle umbo; rib aperture sparse, growth-lines indistinct; ventral interarea apsacline to orthocline, short, delthyrium open, pseudodeltidium reduced; dorsal interarea one-third length of ventral interarea, chilidial plates small, arcuate; teeth subparallel to interarea, slightly crenulated distally; median septum short but high, extending about 1 mm. across ventral umbo and separating indistinct flabellate muscle field; first 2 pairs of spine openings deflected laterally by semiconical screens of secondary shell; cardinal process lobes more or less fused medianly, myophore V-shaped, directed postero-dorsally and fused proximally; deep alveolus flanked by socket ridges at about 20° to hinge-line and extending about one-third its width; lateral ridges short and low posteriorly; shell substance thin, pseudopunctate.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52771)	6·5	8·5
PARATYPES.	Complete pedicle valve (BB.52772)	6·5	9·3
	Incomplete pedicle valve (BB.52773)	—	8·3
	Complete damaged shell (BB.52776)	3·6	*c.* 5·8
	Complete shell (BB.52774)	*c.* 5·0	7·6
	Complete pedicle valve (BB.52775)	5·0	6·6

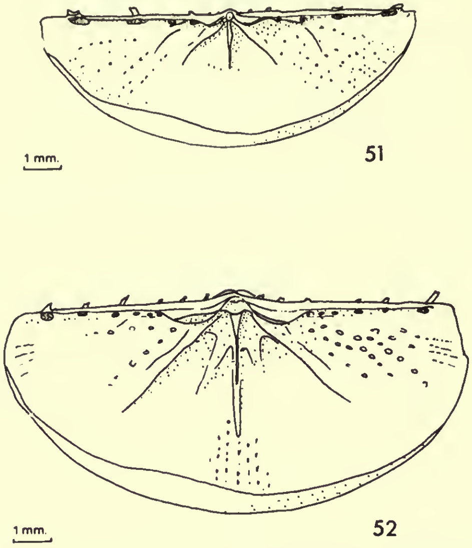
TYPE LOCALITY. Sillees River, about 300 yds east of Bunnahone Lough (Low D zone).

DISCUSSION. The species is similar in estimates of relative length and thickness to *R. silleesi* (Tables 19, 25) with which it occurs. and the two are probably closely related. In other respects, however, there are persistent clear differences. Thus, *R. delicatus* differs from *R. silleesi* in having a much flatter ventral umbo which does not project beyond the hinge-line, which constitutes the greatest width of the shell. The radial ornament, although of similar frequency, is less prominent, the ribs being low and costellae added on the pedicle valve by intercalation and dichotomy rather than almost entirely by dichotomy. The rows of tubercles are uniformly delicate over the entire ventral interior, about 4 occurring per mm. on the lateral flanks, whilst in this region of *R. silleesi* the tubercles are about twice the size with a frequency of 2 or 3 per mm. The dorsal median septum is ill defined and perhaps never fully developed. The body cavity is smaller and the shell substance thinner.

The poorly defined ribbing and its absence close to the posterior margin is similar to the ornamentation of *R. hindi* Muir-Wood from the H zone of Cheshire, and to the poorly ribbed specimens of *R. celticus* Muir-Wood typical of the low E zone of Northumberland. However, the Fermanagh specimens differ from the former species in being concavo-convex, having fewer spines per unit length of hinge-line and in having 7 or 8 ribs per mm. at 4 mm. from the umbo as compared to 5 or 6 per mm. in *R. hindi*. The frequency of ribbing on 5, 13 and 5 specimens attributed to *R. celticus* from Northumberland is 4, 5 and 6 ribs per mm respectively. 4 mm. from the umbo. This frequency is comparable to that of *R. celticus* s.s., but is coarser that that of the two Fermanagh species *R. silleesi* and *R. delicatus*.

The brephic shell was furnished with a supra-apical pedicle sheath (Pl. 9, fig. 14), extending ventro-posteriorly, which arose from the tip of the pedicle beak and posterior to the shallow V-shaped groove across the young shell. During growth each pair of hinge-spines was inserted at fairly regular intervals and projected posteriorly in the commissural plane at the time of their growth. As growth proceeded the commissural plane rotated clockwise relative to the substratum (as viewed laterally with the umbo to the left) so that adult shells have their lateral spines directed posteriorly and their median, early formed spines, project dorsally as in *R. silleesi* (Text-fig. 42). Like *R. silleesi*, the spines retain their connection to the interior, but unlike that species, the interarea is only slightly thickened so that instead of oblique canals maintaining connection, localized deposits of secondary shell deflect the internal openings laterally to positions comparable to those of *R. silleesi* (Text-figs 51, 52). This deflection became less pronounced during growth so that younger spines have more direct openings to the interior. A valve 9·3 mm. wide has its first formed spines 0·5 mm. from the mid-line, but these do not open to the interior for a distance of 1·2 mm. from the mid-line; at this distance the second spines occur and these open internally 1·7 mm. from the mid-line.

The slight amount of secondary shell deposition has resulted in poorly developed internal markings. The ventral muscle field has slight postero-lateral thickenings at its margin, but the median septum is rarely continued as a median ridge. Only two cardinalia are available for study and these have well developed socket ridges at about 20° to the hinge-line, extending about one-third of the hinge-width; the lateral septa (anderidia) are clearly distinguishable, having raised prolongations anteriorly which are considered to have supported the posterior sections of the lophophore. There is no apparent indication of the development of a dorsal median septum, and it is certainly absent at a hinge width of about 8 mm. However, preservation of brachial valves is not sufficiently good to be able to say with certainty that no septum existed in old shells, especially as it is a structure which developed late in the ontogeny of *Rugosochonetes*.



Figs. 51-52. Illustrations of the pedicle valve interior of *Rugosochonetes delicatus* sp. n. (Fig. 51) and *R. silleesi* sp. n. (Fig. 52) showing the difference in the internal spine openings.

Table 25

$\bar{l}$ mm. (var.) = 5·26 (1·367)
$\bar{w}$ mm. (var.) = 7·63 (2·341)
r = 0·980
a (var.) = 1·309 (0·00404)

$\bar{l}$ mm. (var.) = 5·26 (1·367)
$\overline{th}$ mm. (var.) = 1·58 (0·315)
r = 0·803
a (var.) = 0·480 (0·00481)

Table 25. Statistics of length (l), maximum width (w) and thickness (th) of 19 pedicle valves of *Rugosochonetes delicatus* sp. n.

Table 26

Ribs	6	7	8	9
at 2 mm.	4	9	3	3
at 4 mm.	4	8	7	1

Table 26. Number of ribs counted per mm. width at 2 mm. and 4 mm. antero-medianly of the ventral umbo of *R. delicatus* sp. n.

Rugosochonetes transversalis sp. n.

(Pl. 9, figs. 16–25)

DIAGNOSIS. Wide *Rugosochonetes* with semi-elliptical outline, low rounded costellation; median ridges of cardinal process subparallel and narrowly separated; socket ridges prominent and divergent from hinge-line.

DESCRIPTION. Outline transversely semi-elliptical, about one-half as long as wide, umbo flattened, not extending beyond hinge-line which constitutes greatest width of shell; profile concavo-convex, regular, about one-third as deep as long, body cavity narrow, commonly slightly sulcate; hinge-spines irregularly placed at high angle; multicostellate, ribs low rounded with rare apertures, costellae added by dichotomy on both valves, with about 3 ribs occurring per mm. width, 4 mm. antero-medianly from ventral umbo; growth lines indistinct; ventral interarea more or less orthocline, delthyrium about one-third closed by highly arched apical pseudodeltidium; dorsal interarea orthocline to apsacline, about one-half length of ventral interarea, notothyrium with U-shaped chilidium; teeth diverging slightly from interarea; short high median septum separating elongate oval adductor scars, with flanking trigonal diductor scars; median ridge may extend anteriorly from septum for 2 or 3 mm.; two low ridges extend beyond median ridge from anterior ends of adductor scars for about two-thirds valve length (possibly traces of *vascula media*); cardinal process rather wide, median muscle ridges narrowly separated, lateral ridges divergent giving quadrified postero-dorsal surface; sockets deep, anteriorly bordered by prominent socket ridges extending about one-quarter hinge width; adult median septum partly fills alveolus, extending nearly one-half valve length, broad and low, anteriorly raised; lateral septa diverge at 25° from mid-line, and separate elongate oval anterior adductor scars from wider trigonal posterior scars; internally radially tuberculate except postero-laterally; shell substance pseudopunctate.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52778)	13·5	*c.* 23·0
PARATYPES.	Incomplete pedicle valve (BB.52779)	*c.* 11·0	*c.* 22·0
	Incomplete pedicle valve (BB.52781)	5·5	—
	Complete brachial valve (BB.52783)	10·0	19·5

TYPE LOCALITY. Sillees River, about 300 yds east of Bunnahone Lough (Low D zone).

DISCUSSION. The radial ribbing is almost as wide as that found within *Plicochonetes*, as emended by Muir-Wood (1962 : 82), but differs in being poorly defined with low indistinct ribs. Branching is not common but almost invariably by dichotomy. Table 28 shows the distribution of costellation on pedicle valves. Growth lines are indistinct and may be impossible to distinguish on the silicified material. This poorly defined ornamentation cannot be attributed to abrasion, prior to silicification, as delicate structures, such as hinge spines and the pseudodeltidium are preserved, and the concave brachial valves would have been well protected. About one-half of the pedicle valves show sporadic concentric lamellae, probably indicating some irregular retardations of growth. Eight out of twelve shells have a slight median sulcation in their pedicle valves which dies out towards the anterior margin. This folding is even less marked on the brachial valves. Currie (1937 : 423) pointed out that a median sulcation of Chonetacea arose in the mid Carboniferous and it may be that the slight sulcation seen on several of the Fermanagh shells is an indication of this trend.

In outline *R. transversalis* is similar to *C. laguessiana* de Koninck mut. θ Hind from the Gin Mine Marine Band, N. Staffs. (Brit. Mus. (Nat. Hist.) B.47309), but this shell is more finely ribbed, and in this respect is comparable to *R. celticus* s.s. It has about 8 spines in 10 mm. on either side of the umbo which contrasts with 5 or 6 spines in the same distance on the Fermanagh shells. In *R. transversalis* most of the spines retain internal openings, the more medianly placed spines having oblique canals leading to their openings which are lateral of the teeth. The internal surfaces of the ears, and regions immediately anterior of the interareas, are not tuberculate, but the ear regions are irregularly pitted. In old shells, the radial rows of tubercles tend to coalesce into low ridges with the tips of the tubercles still protruding from their crests. The ventral median septum terminates posteriorly in a thickened region between the bases of the teeth and below the apex of the delthyrium, but without the distinctly node-like callus of *R. silleesi*.

The dorsal median septum is typical for the genus in its late development, and the lateral septa are again prominent anteriorly, protruding from the valve floor to the inferred position of the body wall. Like the ventral valve, tuberculation is confined to the mid and lateral regions, and towards the cardinal extremities the pair of slight knobs probably assisted in the articulation of this long-hinged species. Brachial ridges are not clearly distinguishable.

TABLE 27

$\bar{l}$ mm. (var.) = 10·70 (9·6943)
$\bar{w}$ mm. (var.) = 18·78 (40·640)
r = 0·578
a (var.) = 2·048 (0·0465)

$\bar{l}$ mm. (var.) = 10·70 (9·694)
$\overline{th}$ mm. (var.) = 3·77 (4·257)
r = 0·770
a (var.) = 0·663 (0·0298)

TABLE 27. Statistics of length (l), maximum width (w) and thickness (th) of 8 shells or pedicle valves of *Rugosochonetes transversalis* sp. n.

TABLE 28

Ribs	3	4	5
at 2 mm.	0	6	5
at 4 mm.	9	3	0

TABLE 28. Number of ribs counted in 1 mm. width at 2 and 4 mm. antero-medianly from the pedicle umbo of *Rugosochonetes transversalis* sp. n.

Genus ***PLICOCHONETES*** Paeckelmann, 1930

TYPE SPECIES. *Chonetes buchianus* de Koninck, 1843, by original designation of Paeckelmann (1930 : 222).

Plicochonetes buchianus (de Konick)

(Pl. 9, figs. 27–32)

DIAGNOSIS (emended). Strong concavo-convex *Plicochonetes* with narrow body cavity; prominent rounded ribs, not developed postero-laterally; small pseudodeltidium and chilidial plates present; dorsal median septum short and low.

DESCRIPTION. Outline subsemicircular with straight hinge-line at widest part of shell, about two-thirds as long as wide; ears well developed and smooth; profile concavo-convex with narrow body cavity, shell about one-half as deep as long; radial ornament prominent and evenly developed from about 16 costae with rare additions of ribs by branching on pedicle valves and intercalation on brachial valves, about 5 ribs per 2·5 mm. at 4 mm. from ventral umbo, rib-apertures sparsely developed on both valves; growth lines finely developed; ventral interarea concave, more or less orthocline, delthyrium closed apically by small arched pseudodeltidium; at least seven pairs of hinge spines subparallel to mid-line; dorsal interarea hypercline with notothyrium similarly sized to delthyrium and flanked by prominent chilidial plates; teeth suboval in outline; short high median septum extending as low ridge between elongately oval adductor scars; diductor scars poorly impressed; cardinal process bilobed and medianly fused, external face quadrifid with prominent median muscle boundaries separated by narrow groove; socket ridges extending about one-third hinge-line width; median septum low and broad, raised anteriorly and extending about one-quarter valve length, but continued as short ridge; lateral septa at 25° to 30° from mid-line, commonly prominent anteriorly; brachial impressions lobate, extending about three-fifths valve length and disc width; shell substance thin.

MEASUREMENTS (in mm.):

	length	width
Complete shell (BB.52917)	7·8	12·8
Incomplete brachial valve (BB.52918)	10·6	*c.* 16·0
Incomplete brachial valve (BB.52919)	6·9	—

DISCUSSION. The species is rarely found in the limestones from Co. Fermanagh, but a few well preserved specimens warrant discussion.

The genus was inadequately described by Paeckelmann (1930). In her description of the genus Muir-Wood (1962 : 82) makes no mention of the presence of chilidial plates. These are well developed arching the lateral flanks of the external face of the cardinal process so as partially to obscure the lateral muscle boundary ridges (Pl. 9, fig. 30). The plates are barely fused medianly, but were well developed when the valve was 6 mm. long. The presence of a well defined apical pseudodeltidium in the present material indicates that this structure may be commoner on well preserved material than has been thought. This structure, together with the chilidial plates should be noted within a diagnosis of *Plicochonetes*.

The correspondence between the ribbing of the brachial and pedicle valves is indicated by the way in which costellae are commonly added by intercalation on the brachial valve in a position opposite to a branched rib on the pedicle valve. An example of this can be seen on the shell illustrated on Pl. 9, figs. 29, 30. This is considered to be a common feature of ribbing, and is a necessity for a close fit of the anterior margin, but is difficult to demonstrate on more finely ribbed groups.

Rib apertures are developed both on the ribs and sparsely on the smooth ears in a radial fashion. These structures are more fully discussed under *Rugosochonetes*.

In common with other chonetaceids, the lateral septa developed at an early stage, prior to the differentitation of the median septum or clear development of the adductor scars (Pl. 9, fig. 31). Their prominence indicates a functional importance and their prolonged anterior extremities probably assisted in the support of the lophophore at the body wall as in *Rugosochonetes*.

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EXPLANATION OF PLATES

Unless otherwise stated, all the specimens are housed in the British Museum (Nat. Hist.); were collected from the silicified limestone of Co. Fermanagh, and have been sprayed with ammonium chloride immediately prior to being photographed.

PLATE 1

Crania quadrata (M'Coy)

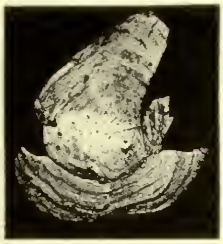
Figs. 1, 2. External and internal views of broken brachial valve. BB.55599. ×1·5.
Fig. 3. External view of brachial valve. BB.55601. ×4·0.
Figs. 4, 5. External and internal views of brachial valve. BB.55600. ×2·1.
Figs. 6, 7. Dorsal and lateral views of brachial valve. BB.55616. ×6·2.
Fig. 8. External view of brachial valve. BB.55602. ×5·8.
Fig. 9. External view of brachial valve. BB.55603. ×5·2.

Acanthocrania cf. *laevis* (Keyes)

Fig. 10. External view of brachial valve. BB.55605. ×3·1.
Fig. 11. External view of fragment of brachial valve. BB.55606. ×2·9.
Figs. 12–14. Lateral, dorsal and internal views of brachial valve. BB.55604. ×3·0.

Philhedra trigonalis (M'Coy)

Figs. 15, 16. Dorsal and lateral view of brachial valve attached to a rugosochoneteid BB. 55607. ×2·0.
Figs. 17, 18. Lateral and dorsal views of brachial valve. BB.55608. ×2·0.
Figs. 19–21. Lateral, internal (×2·5) and dorsal views of brachial valve. BB.55610. ×2·0.
Figs. 22, 23. Internal and lateral views of brachial valve. BB.55609. ×2·0.
Figs. 24–26. Internal, dorsal and lateral views of brachial valve. BB.55611. ×2·0.
Figs. 27–29. Lateral, dorsal and internal views of brachial valve with a small portion of the pedicle valve still attached. BB.55612. ×2·0, ×2·3 and ×3·5 respectively.
Figs. 30, 31. Internal and external views of brachial valve. BB.55614. ×5·2.
Figs. 32, 33. Dorsal and lateral views of brachial valve. BB.55613, ×3·0.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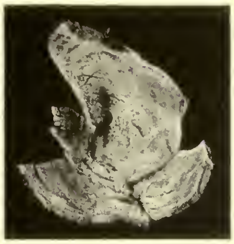
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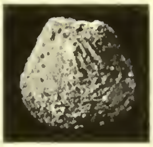
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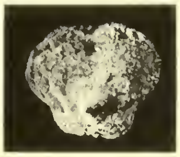
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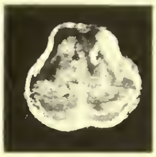
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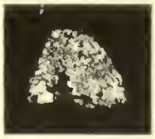
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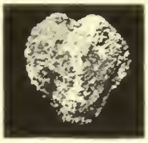
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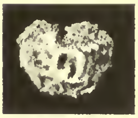
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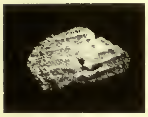
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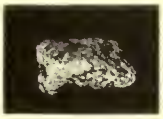
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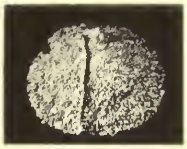
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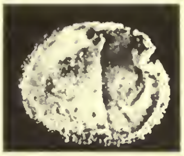
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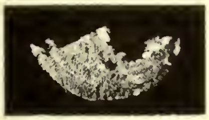
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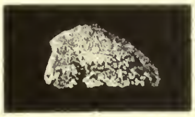
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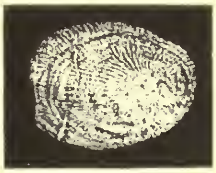
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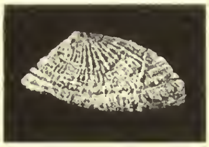
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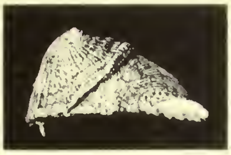
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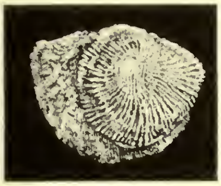
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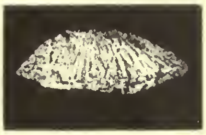
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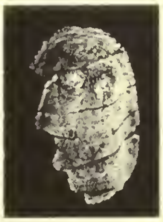
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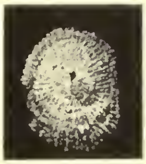
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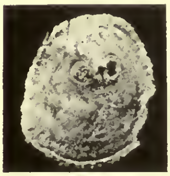
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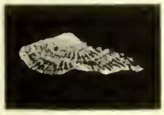
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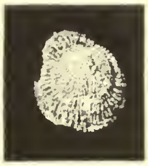
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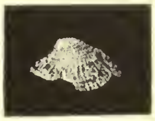
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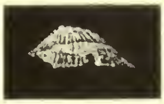
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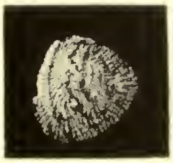
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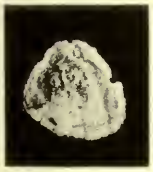
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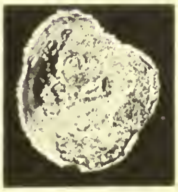
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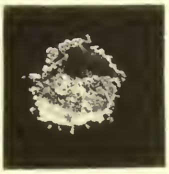
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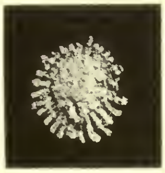
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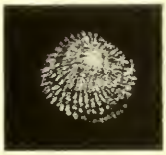
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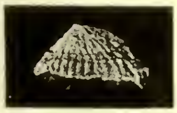
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PLATE 2

Schizophoria resupinata (Martin)

FIGS. 1–3. Neotype, from Bolland (Gilbertson Colln.) viewed dorsally, ventrally and anteriorly. BB.2420. ×0·5.

FIGS. 4, 5. Part of brachial valve from the Visean of Cam Back, Yorks., viewed externally (×0·5) and internally (×0·95). B.56088.

FIG. 6. Part of brachial valve from the Visean of Ulverstone, Lancs., showing the trilobed cardinal process and fulcral plates. 30113. ×0·95.

Schizophoria resupinata dorsosinuata Demanet

FIGS. 7–11. Incomplete shell viewed dorsally, ventrally, laterally, posteriorly and anteriorly. BB.52701. ×1·6.

FIGS. 12, 13. Incomplete shell viewed postero-ventrally and dorsally. BB.52702. ×1·6.

FIG. 14. Incomplete brachial valve cardinalia. BB.52710. ×2·7.

FIGS. 15, 16. Incomplete pedicle valve viewed posteriorly and dorsally. BB.52704. ×2·3.

FIG. 17. Cardinalia of brachial valve. BB.52705. ×4·0.

FIG. 18. Ventral view of incomplete young brachial valve. BB.52712. ×3·3.

FIG. 19. Ventral view of incomplete young brachial valve. BB.52706. ×6·0.

FIG. 20. Incomplete brachial valve interior. BB.52922. ×5·0.

FIG. 21. Incomplete brachial valve interior. BB.52933. ×2·0.

FIGS. 22–25. Young shell viewed posteriorly, anteriorly, dorsally and ventrally. BB.52716. ×6·0.

FIGS. 26, 27. Young pedicle valve interior and exterior. BB.52714. ×3·1.

FIGS. 28, 29. Young brachial valve exterior and interior. BB.52708. ×6·0.

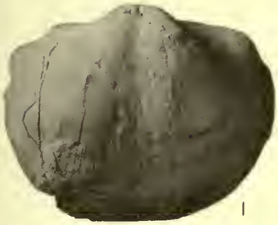
FIG. 30. Juvenile brachial valve interior. BB.52707. ×6·0.

FIGS. 31, 32. Juvenile pedicle valve exterior (×6·5) and interior (×8·5) BB.52713.

FIGS. 33–36. Juvenile shell viewed ventrally, dorsally, anteriorly and posteriorly. BB.52717 ×8·75.

FIG. 37. Incomplete brachial valve interior. BB.52715. ×2·3.

PLATE 2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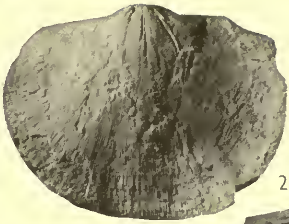
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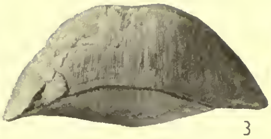
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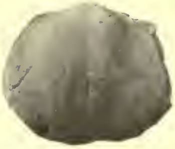
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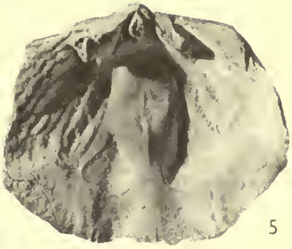
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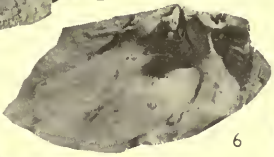
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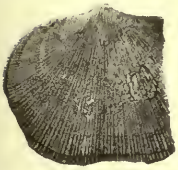
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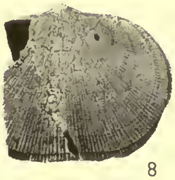
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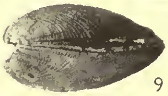
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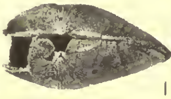
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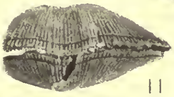
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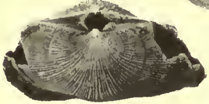
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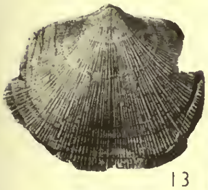
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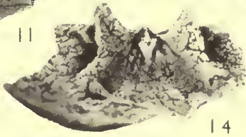
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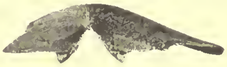
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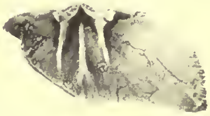
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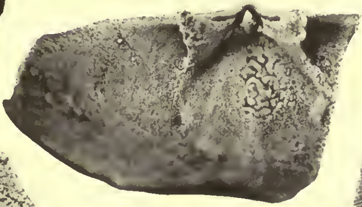
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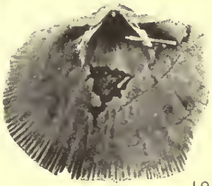
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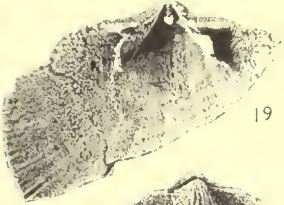
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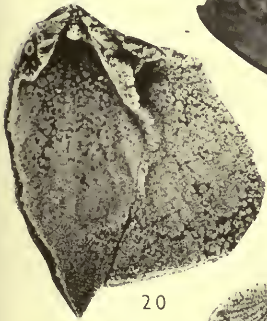
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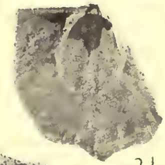
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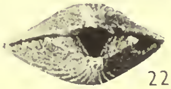
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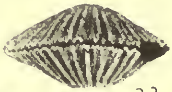
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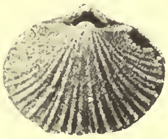
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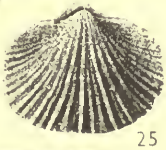
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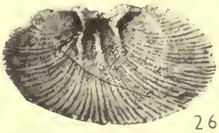
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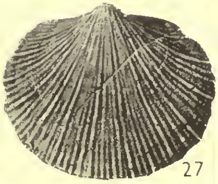
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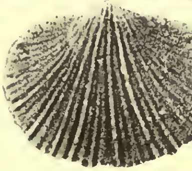
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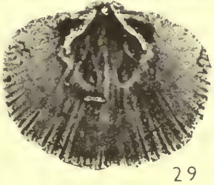
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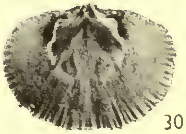
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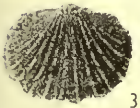
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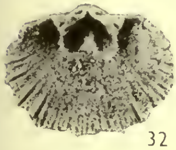
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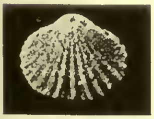
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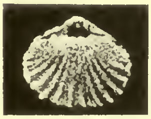
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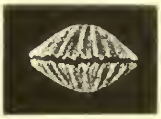
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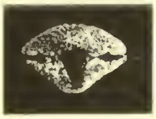
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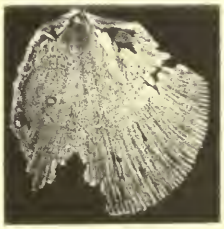
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PLATE 3

Rhipidomella michelini (L'Eveillé)

Figs. 1–3. Complete topotypic shell from Tournai, Belgium, viewed ventrally, dorsally and posteriorly. BB.55617 (reregd. from B.18254). ×1·1.

Figs. 4, 5. Brachial valve, from Tournai, Belgium, viewed antero-ventrally and ventrally. BB.55618. ×1·1.

Fig. 6. Pedicle valve interior, from Tournai, Belgium, BB.55619. ×1·1.

Figs. 7–10. Complete shell viewed dorsally, ventrally, laterally and posteriorly. BB.52718. ×2·4.

Figs. 11, 12. Incomplete pedicle valve viewed dorso-laterally and dorsally. BB.52719. ×3·5.

Figs. 13, 14. Posterior portion of shell viewed internally and externally. BB.52727. ×4·5.

Figs. 15–18. Brachial valve exterior, interior (×2·87), posterior (×3·8) and lateral (×2·8) views. BB.52722.

Figs. 19, 20. Pedicle valve exterior (×2·5) and interior (×3·0) BB.52720.

Figs. 21, 22. Juvenile shell viewed dorsally and ventrally. BB.52724. ×3·8.

Fig. 23. Incomplete brachial valve cardinalia. BB.52728. ×3·5.

Figs. 24, 25. Juvenile brachial valve exterior and interior. BB.52726. ×4·5.

Leptagonia analogia (Phillips)

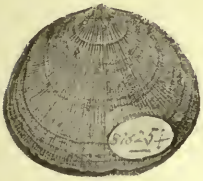
Figs. 26, 27. Lectotype from the lower Carboniferous of Bolland, in the Gilbertson Colln. viewed dorsally and ventrally. B.8936. ×1·0.

Fig. 28. Incomplete pedicle valve interior, from the lower Carboniferous Redesdale limestone, Northumberland. BB.46524. ×3·0.

Figs. 29, 30. Internal mould, retaining fragments of shell, viewed anteriorly and dorsally, from the Gilbertson Colln. BB.55777. ×1·0.

Fig. 31. Complete shell from the Lower Carboniferous of Carrick-on-Shannon, Eire, viewed ventrally. Hunterian Museum L.3817/1. ×1·0.

PLATE 3



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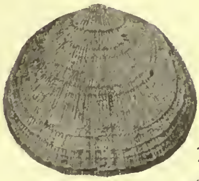
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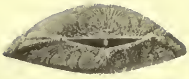
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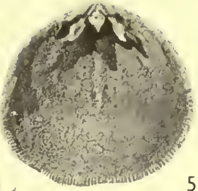
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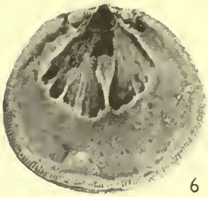
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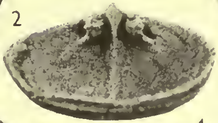
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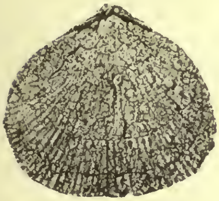
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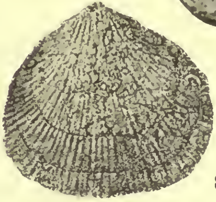
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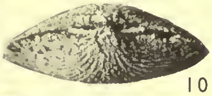
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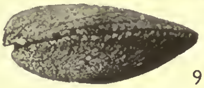
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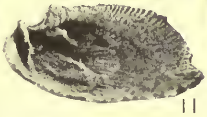
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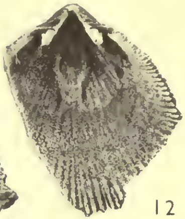
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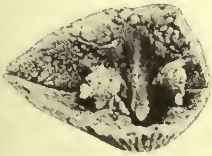
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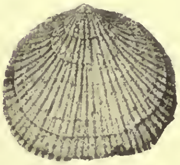
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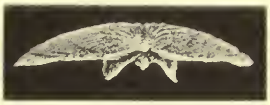
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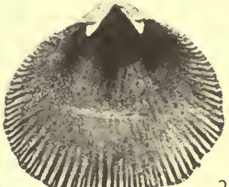
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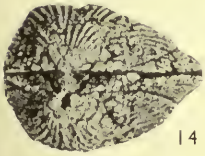
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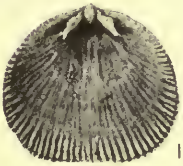
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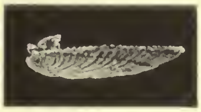
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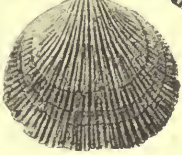
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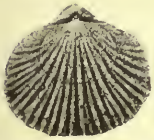
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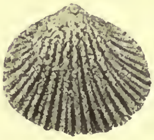
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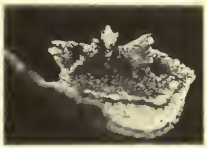
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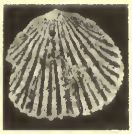
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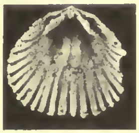
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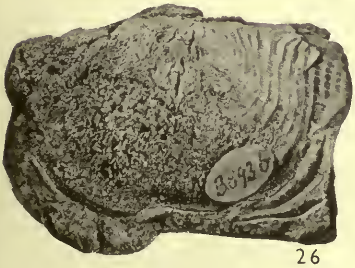

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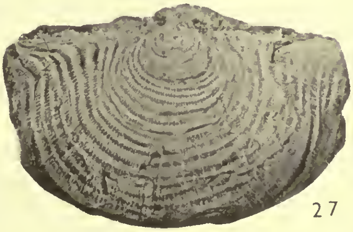
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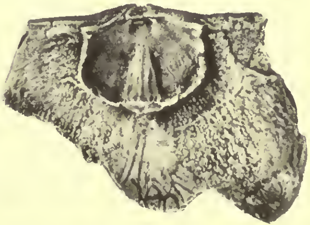
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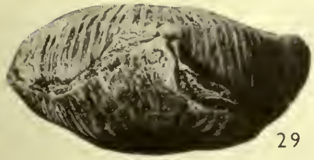
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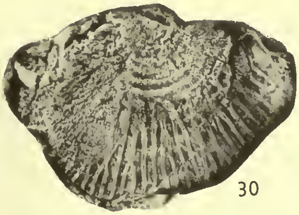
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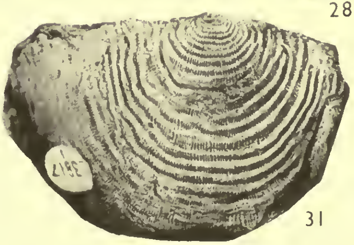

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PLATE 4

Leptagonia analoga (Phillips)

FIG. 1. Brachial valve cardinalia from Carrick-on-Shannon. Hunterian Mus., L.3834/22. × 3·0.

FIG. 2. Brachial valve interior from Redesdale, Northumberland showing a mature cardinalia and saccate pallial sinuses. B.43708. × 1·1.

FIG. 3. Incomplete silicified brachial valve exterior. BB.52921. × 3·4.

FIGS. 4, 5. Juvenile shell viewed dorsally (× 5·0) and ventrally (× 3·4). BB.52729.

FIGS. 6, 7. Juvenile brachial valve interior and exterior. BB.52730. × 5·0.

FIGS. 8, 9. Incomplete brachial valve from the Lower Carboniferous of Co. Sligo viewed posteriorly (× 1·3) and ventrally (× 0·9). BB.52731.

Derbyoides nebrascensis Dunbar & Condra

FIGS. 10–12. Topotypic incomplete pedicle valve from the Upper Carboniferous near Nehawka, Nebraska, viewed externally, anterodorsally and dorsally. BB.55491. × 1·0.

FIGS. 13, 14. Topotypic incomplete brachial valve exterior and interior. BB.55490. × 1·0.

Tapajotia tapojotensis (Derby)

FIGS. 15, 16. Topotypic incomplete pedicle valve from the Upper Carboniferous of Rio Tapajos, Brazil, viewed dorsally and anterodorsally. BB.55493. × 1·0.

FIGS. 17–19. Topotypic young pedicle valve viewed antero-dorsally, dorsally and ventrally. BB.55496. × 2·1.

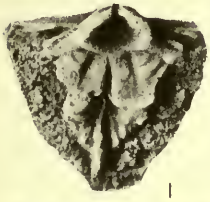
FIGS. 20, 21. Topotypic incomplete brachial valve viewed posteriorly and ventrally. BB.55494. × 1·5.

FIGS. 22, 23. Topotypic young brachial valve exterior and interior. BB.55495. × 2·1.

Brochocarina wexfordensis (Smyth)

FIG. 24. Paratype. Incomplete pedicle valve interior from Hook Head, Co. Wexford. Trinity College Dublin Colln. × 0·75.

FIGS. 25, 26. Holotype. Brachial valve viewed posteriorly (× 1·3) and externally (× 0·7). Trinity College Dublin Colln.



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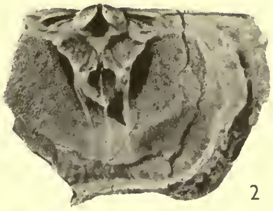

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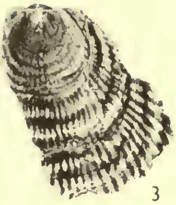

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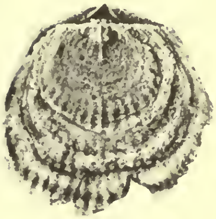

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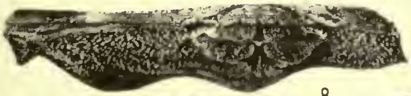

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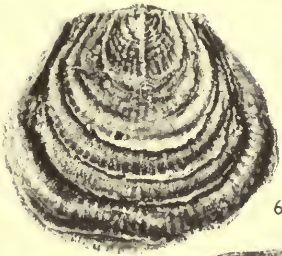

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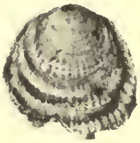

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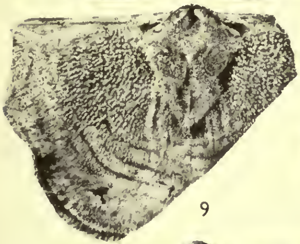

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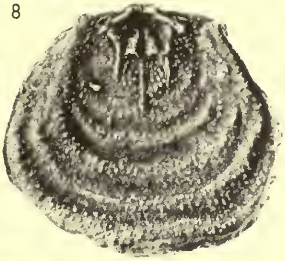

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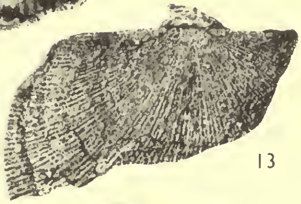

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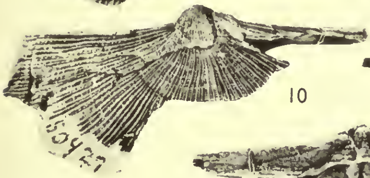

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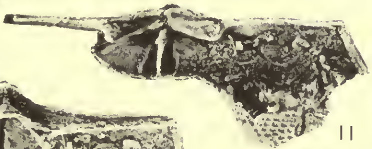

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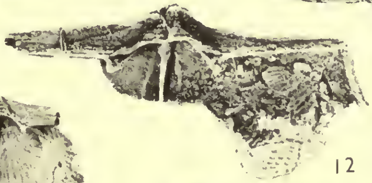

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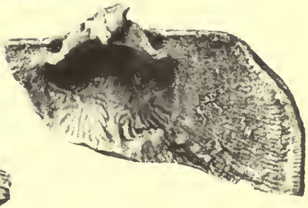

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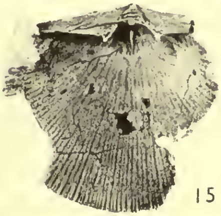

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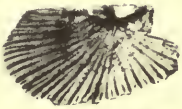

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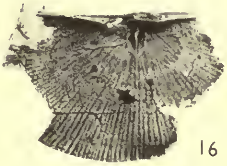

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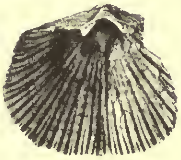

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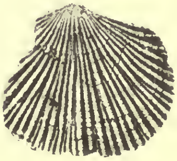

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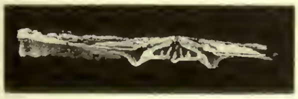

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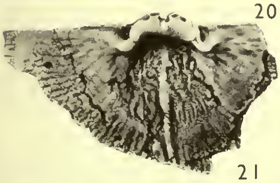

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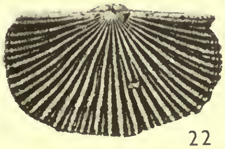

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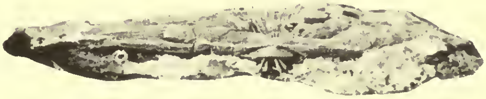

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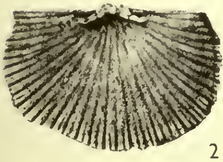

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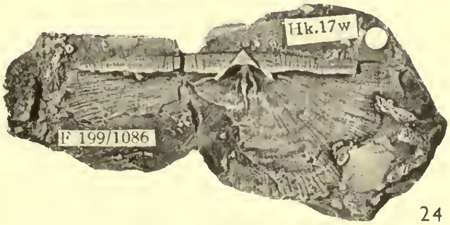

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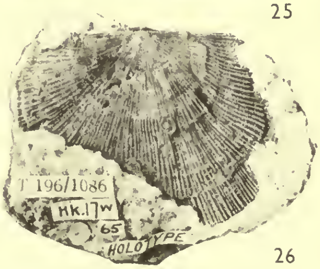

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HOLOTYPE

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PLATE 5

Brochocarina wexfordensis (Smyth)

FIGS. 1, 2. Incomplete pedicle valve exterior and interior. BB.55779. ×1·0.

FIGS. 3, 4. Pedicle valve exterior and interior. BB.55598. ×0·75.

FIG. 5. Incomplete pedicle valve interior. BB.55778. ×1·0.

FIG. 6. Incomplete shell viewed postero-dorsally. BB.55597. ×1·5.

FIG. 7. Incomplete pedicle valve interior. BB.52733. ×1·7.

FIG. 8. Juvenile pedicle valve interior. BB.52734. ×2·7.

FIGS. 9, 10. Juvenile brachial valve exterior and interior. BB.55596. ×2·0.

FIGS. 11–13. Incomplete pedicle valve exterior (×0·8) detail of external ornamentation (×3·0) and interior (×0·8). BB.52732.

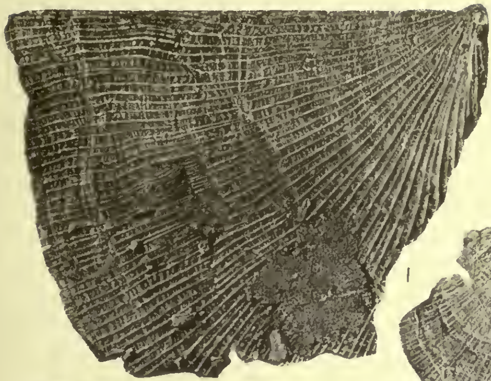
FIGS. 16, 17. Adult cardinalia viewed ventrally and posteriorly. BB.55595. ×3·0.

FIG. 18. Partially crushed shell from Bundoran, Co. Donegal, showing posterior view of cardinal process and chilidium. BB.52738. ×1·8 (not silicified).

FIG. 19. Incomplete shell from Poll More, near Boho, Co. Fermanagh, showing the ventral interarea. BB.52737. ×1·6 (not silicified).

FIGS. 20, 21. Juvenile brachial valve interior and exteroir. BB.55594. ×4·0.

FIGS. 22, 23. Juvenile brachial valve interior and exterior. BB.55593. ×3·0.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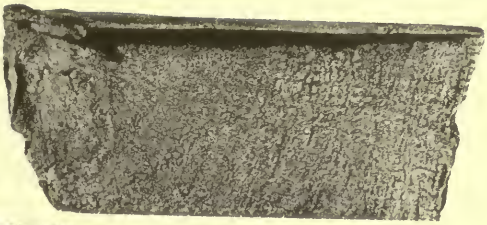
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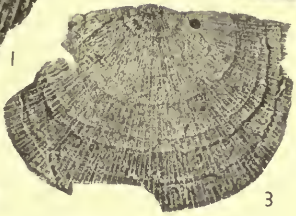
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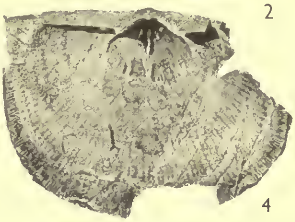
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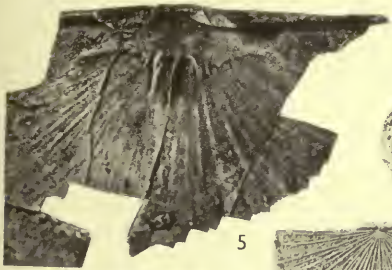
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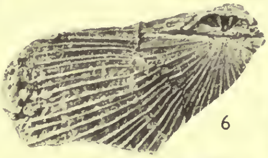
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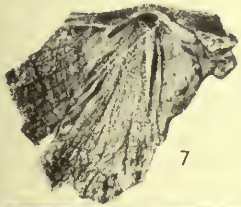
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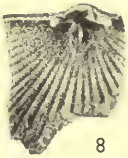
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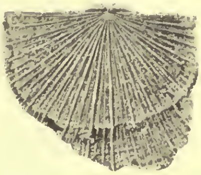
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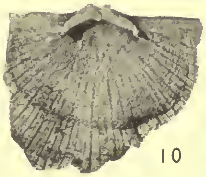
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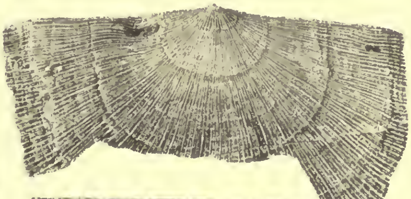
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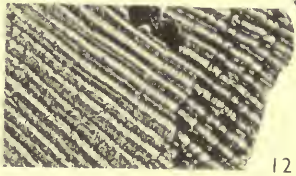
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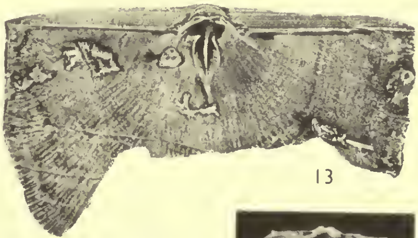
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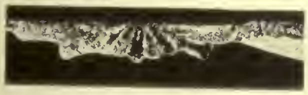
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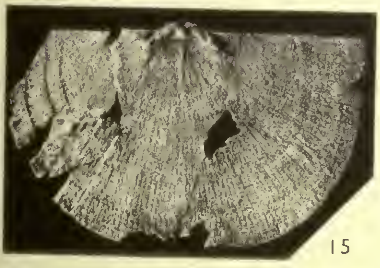
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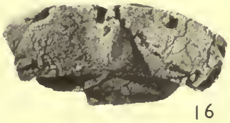
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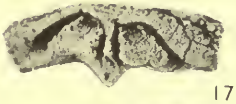
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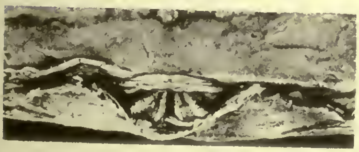
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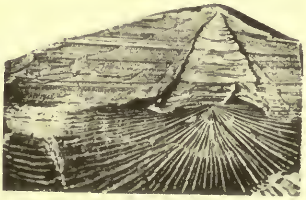
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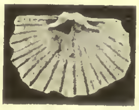
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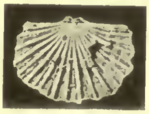
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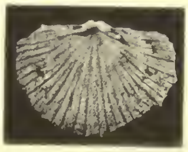
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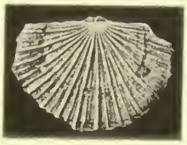
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PLATE 6

Serratocrista fistulosa sp. n.

FIGS. 1–3. Holotype. Complete shell viewed dorsally and ventrally (× 1·8) and detail of external ornamentation (× 6·0). BB. 52739.

FIG. 4. Pedicle valve interior. BB.52741. × 1·6.

FIG. 5. Incomplete brachial valve interior. BB.52743. × 1·7.

FIG. 6. Young brachial valve interior. BB.52740. × 1·8.

FIG. 7. Juvenile pedicle valve exterior. BB.52744. × 4·4.

FIG. 8. Incomplete pedicle valve interior. BB.52742. × 1·7.

FIGS. 9, 10. Incomplete brachial valve exterior and interior. BB.55488. × 2·2.

FIGS. 11, 12. Fragment of pedicle valve viewed laterally and dorsally. BB.55489. × 2·2.

Schellwienella radialis (Phillips)

FIGS. 13–16. Brachial valve viewed externally, internally and laterally (× 1·3) and detail of the external ornamentation (× 2·3). BB.52747.

FIG. 17. Incomplete pedicle valve viewed antero-dorsally. BB.52745. × 3·2.

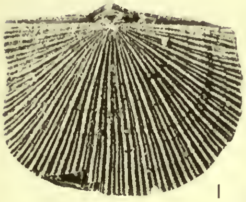
FIG. 18. Juvenile brachial valve interior. BB.52746. × 2·6.

FIG. 19. Detail of external ornamentation on a crushed, unsilicified specimen from Bohenvy, about 1½ miles north of the Sillees R. locality. BB.52750. × 2·4.

FIG. 20, 21. Brachial valve viewed posteriorly and ventrally. BB.52748. × 1·6.

FIGS. 22, 23. Brachial valve cardinalia from Bohenvy, internally (× 1·1) and externally (× 1·7). BB.52749 (unsilicified).

FIG. 24. Holotype. Brachial valve exterior, collected from Florence Court, Co. Fermanagh. The University Museum, Oxford. E.2054. × 1·0.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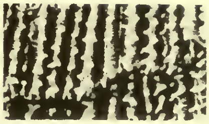
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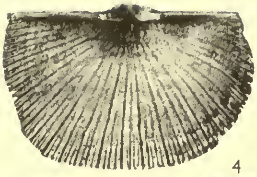
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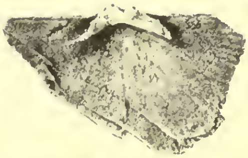
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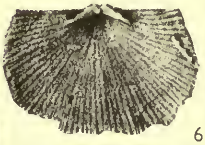
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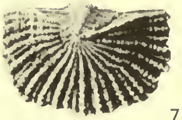
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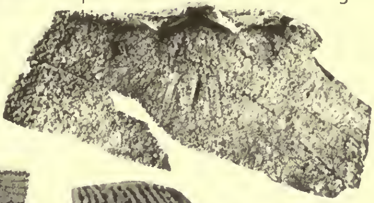
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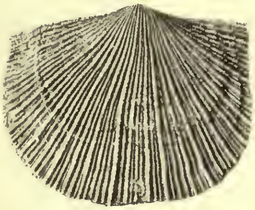
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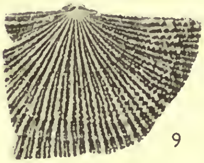
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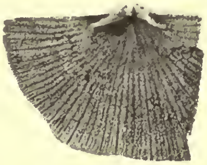
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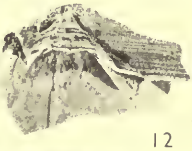
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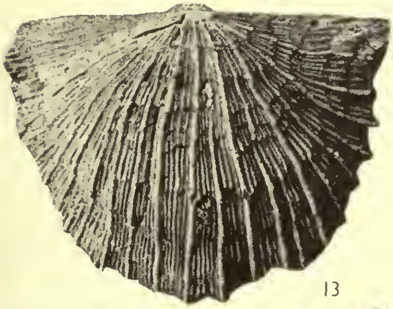
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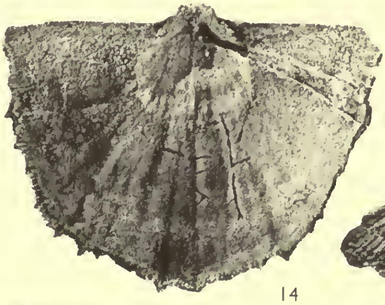
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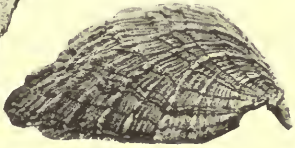
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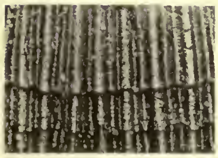
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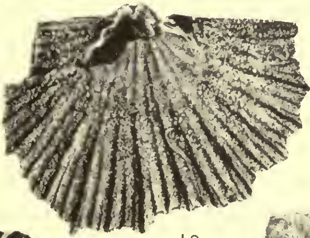
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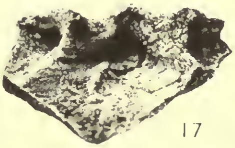
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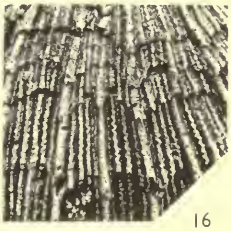
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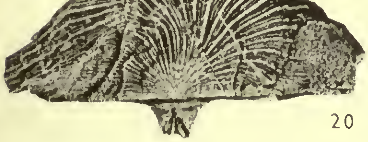
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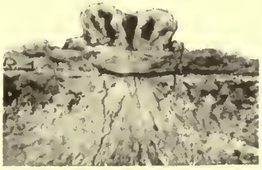
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PLATE 7

Orthotetinid gen. et. sp. indet.

FIGS. 1, 2. Juvenile incomplete brachial valve exterior and interior. BB.55782. ×1·9.

FIGS. 3, 4. Incomplete brachial valve exterior and internal view of cardinalia. BB.55780. ×1·0.

FIGS. 5–7. Dorsal cardinalia viewed dorsally, ventrally and posteriorly showing the complete chilidium. BB.55781. +1·0.

Globosochonetes parseptus sp. n.

FIGS. 8–11. Complete shell viewed dorsally, ventrally, posteriorly and anteriorly. BB.55498. ×5·7.

FIGS. 12–14. Complete pedicle valve viewed externally, dorsally and antero-dorsally to show the short median septum. BB.52752. ×7·5.

FIGS. 15–18. Holotype. Complete, disarticulated shell viewed posteriorly, dorsally, ventrally and laterally. BB.52751. ×7·5.

FIGS. 19, 20. Incomplete shell viewed ventrally and dorsally. BB.55783. ×6·4.

FIG. 21. Incomplete adult brachial valve interior showing short median septum. BB.52754. ×7·7.

FIG. 22. Incomplete brachial valve interior. BB.52753. ×7·5.

FIG. 23. Juvenile pedicle valve viewed posteriorly to show pedicle sheath. BB.52757. ×10·1.

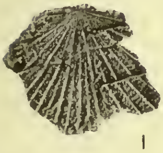
FIG. 24. Young pedicle valve viewed posteriorly to show pedicle sheath. BB.52756,. ×7·5.

FIG. 25. Juvenile brachial valve interior. BB.52755. ×11·5.

FIGS. 26, 27. Young brachial valve with damaged accessory septum, interior and exterior. BB.55499. ×5·5.

Rugosochonetes celticus Muir-Wood

FIGS. 28, 30. Holotype. Complete shell from the Visean of Flint, N. Wales, viewed ventrally, anteriorly, posteriorly and dorsally. BB.41145. ×2·0.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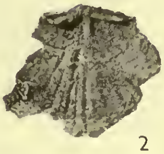
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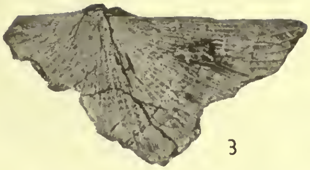
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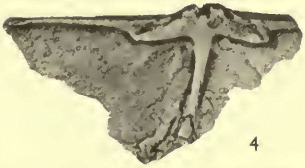
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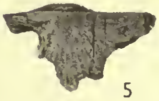
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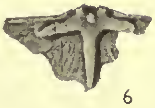
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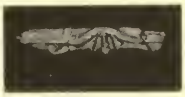
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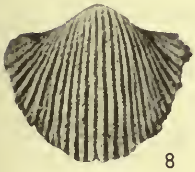
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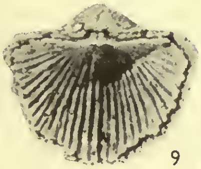
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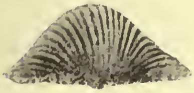
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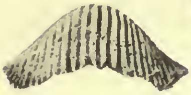
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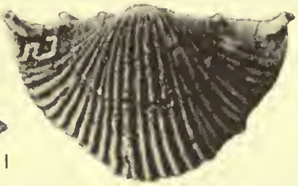
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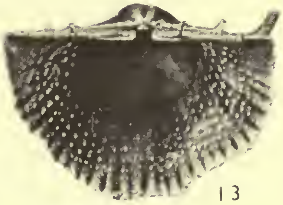
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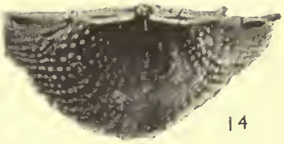
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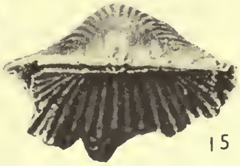
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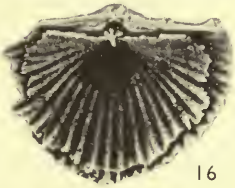
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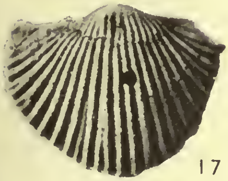
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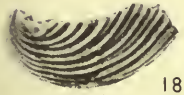
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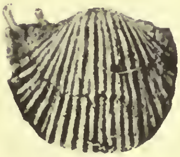
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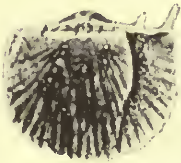
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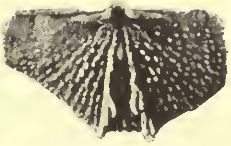
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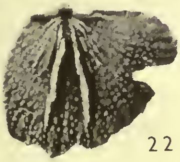
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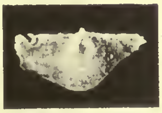
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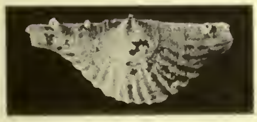
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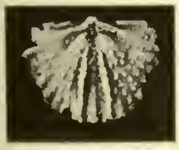
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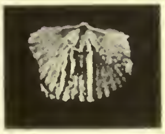
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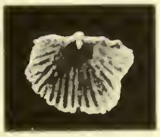
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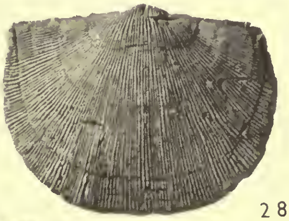
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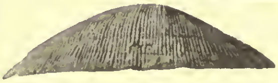
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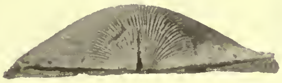
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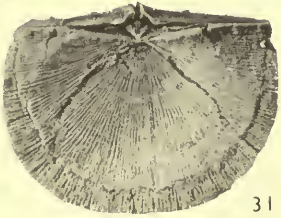
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PLATE 8

Rugosochonetes celticus Muir-Wood

FIG. 1. Complete shell viewed ventrally, identical to holotype and collected from the Lower Carboniferous of Cam Beck, Yorkshire. B.48887. ×2·0.

FIGS. 2, 3. Complete pedicle valve exterior and interior, also from Cam Beck, but of the coarsely ribbed group. B.48894. ×2·0.

FIGS. 4, 5. Pedicle valve interior and exterior of coarsely ribbed specimen from the Visean of Beith, Ayrshire. B.53892. ×2·0.

FIGS. 6, 7. Dorsal and ventral views of poorly ribbed specimen from the Visean of Ancroft, Northumberland. BB.42045. ×2·0.

FIGS. 8, 9. Ventral and dorsal view of similar specimen from Aycroft. BB.42046. ×2·0.

Rugosochonetes silleesi sp. n.

FIGS. 10–13. Holotype. Complete shell viewed dorsally, ventrally, posteriorly and laterally. BB.52758. ×1·7.

FIGS. 14, 15. Complete brachial valve exterior and interior. BB.52761. ×2·4.

FIG. 16. Incomplete brachial valve interior. BB.52762. ×2·9.

FIGS. 17, 18. Pedicle valve viewed antero-dorsally and dorsally. BB.52759. ×2·7.

FIG. 19. Incomplete shell viewed dorsally. BB.52770. ×5·0.

FIG. 20. Juvenile brachial valve interior. BB.52763. ×7·5.

FIG. 21. Young pedicle valve interior. BB.52765. ×3·0.

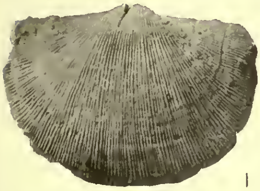
FIG. 22. Pedicle valve interior viewed anteriorly. BB.52760. ×2·7.

FIGS. 23, 24. Incomplete brachial valve viewed postero-ventrally and postero-dorsally. BB.52764. ×3·0.

FIG. 25. Shell viewed postero-dorsally. BB.52766. ×2·7.

FIG. 26. Juvenile pedicle valve exterior showing pedicle sheath. BB.52768. ×7·5.

FIG. 27. Young pedicle valve interior. BB.52767. ×4·1.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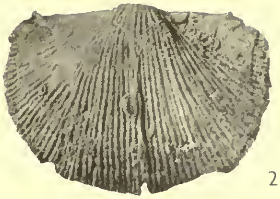
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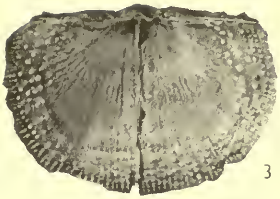
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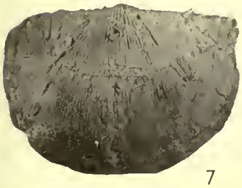
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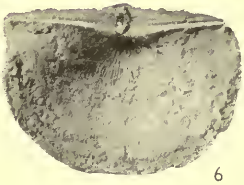
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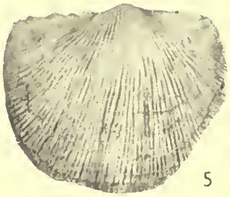
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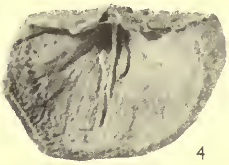
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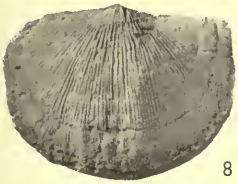
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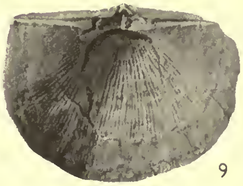
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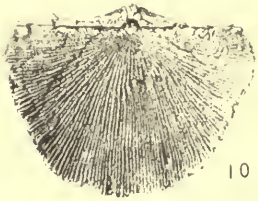
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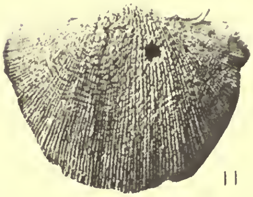
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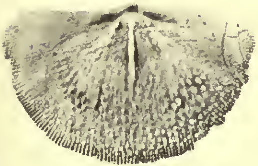
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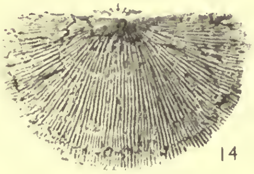
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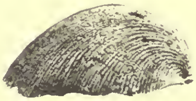
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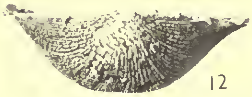
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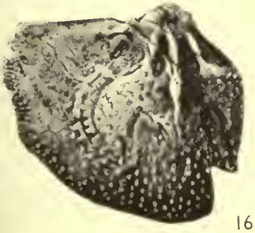
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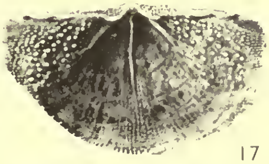
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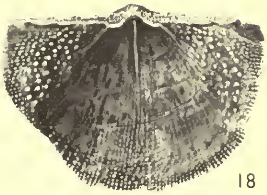
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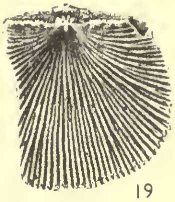
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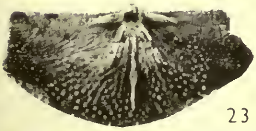
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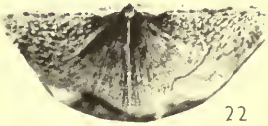
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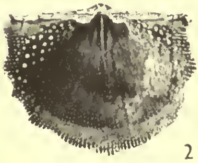
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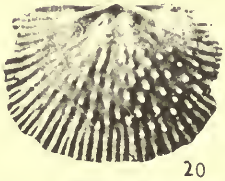
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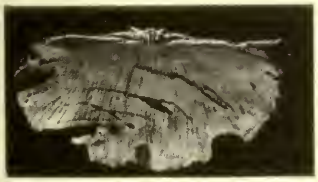
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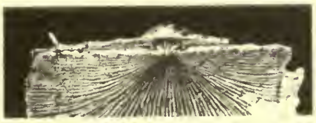
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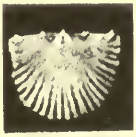
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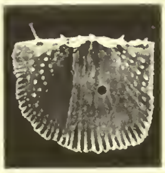
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PLATE 9

Rugosochonetes silleesi sp. n.

Figs. 1, 2. Two unsilicified slightly crushed shells from the shale below the silicified limestone at the Sillees river to show shell ornamentation. BB.52769. (×2·75), BB.55784 (×2·4) respectively.

Rugosochonetes delicatus sp. n.

Figs. 3–5. Holotype. Incomplete shell viewed ventrally, dorsally and laterally. BB.52771. ×3·75.

Figs. 6, 7. Complete shell viewed dorsally and ventrally BB.52774. ×3·8.

Figs. 8–10. Incomplete pedicle valve viewed ventrally, anteriorly and posteriorly. BB.52773. ×3·75.

Fig. 11. Pedicle valve exterior. BB.52775. ×3.75.

Figs. 12, 13. Pedicle valve viewed antero-dorsally and dorsally. BB.52772. ×3.7.

Fig. 14. Crushed juvenile shell with pedicle sheath, viewed ventrally. BB.52776. ×3.75.

Fig. 15. Incomplete brachial valve interior. BB.52777. ×5.0.

Rugosochonetes transversalis sp. n.

Fig. 16. Fragment of brachial valve interior. BB.52784. ×2.7.

Figs. 17, 18. Incomplete pedicle valve viewed anteriorly and dorsally. BB.52779. ×1.7.

Figs. 19-22. Holotype. Incomplete shell viewed posteriorly dorsally, ventrally and laterally. BB.52778. ×1.6.

Fig. 23. Brachial valve interior. BB.52783. ×1.7.

Figs. 24, 25. Dorsal cardinalia viewed ventrally and posteriorly. BB.52785. ×2.75.

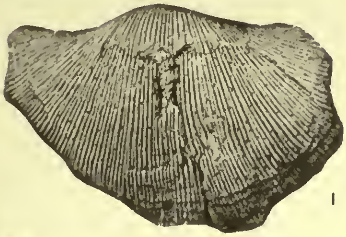
Fig. 26. Incomplete young pedicle valve interior. BB.52781. ×2.75.

Plicochonetes buchianus (de Koninck)

Figs. 27-30. Shell viewed ventrally, laterally, postero-ventrally and dorsally. BB.52917. ×2.4.

Fig. 31. Incomplete juvenile brachial valve interior. BB.52919. ×2.4.

Fig. 32. Incomplete valve interior. BB.52918. ×2.4.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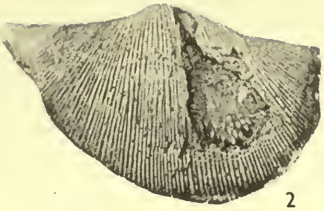
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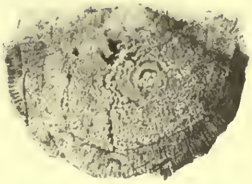
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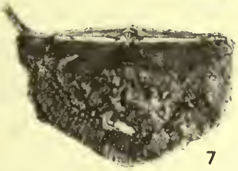
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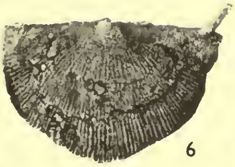
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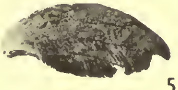
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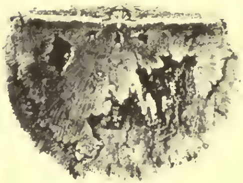
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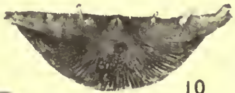
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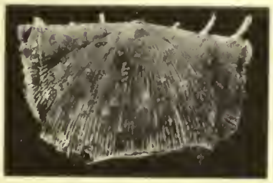
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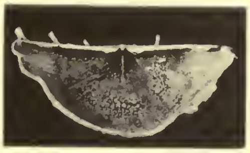
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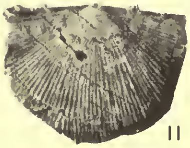
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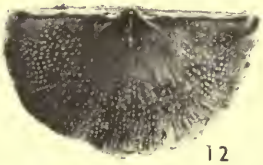
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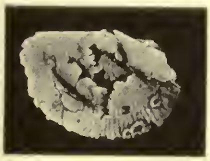
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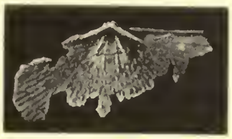
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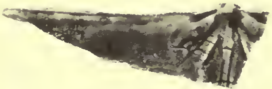
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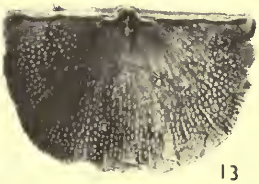
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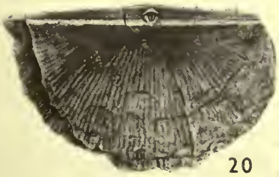
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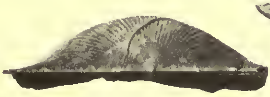
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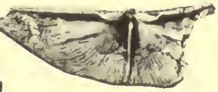
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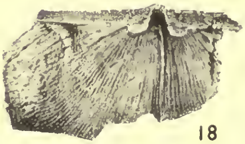
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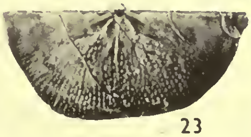
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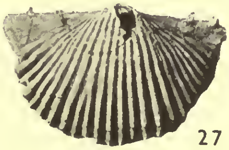
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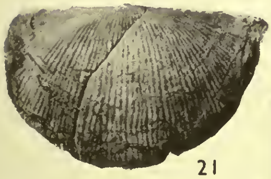
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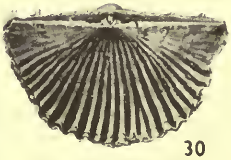
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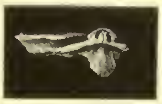
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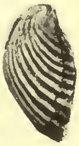
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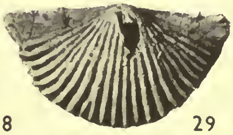
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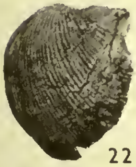
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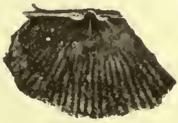
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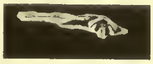
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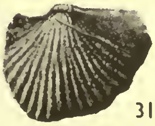
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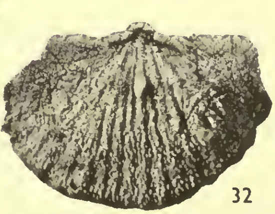
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C. G. ADAMS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 2
LONDON: 1968

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BY

C. G. ADAMS
British Museum (Natural History)

Pp. 71–97; 6 *Plates;* 3 *Text-figures*

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By C. G. ADAMS

MS accepted May 12th 1967

ABSTRACT

The known species of *Austrotrillina* are redescribed and compared, and their geographical and stratigraphical distributions are discussed. It is concluded that the evolutionary changes observed in the wall structure are of value in stratigraphy. One new species, *A. asmariensis*, is erected.

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I. INTRODUCTION

Austrotrillina has long been recognized as an important mid-Tertiary index fossil in the Tethyan and Indo-Pacific regions. It is unknown from the Americas. Unfortunately, the four species so far described, *A. howchini* (Schlumberger), *A. paucialveolata* Grimsdale, *A. brunni* Marie, and *A. striata* Todd & Post, have never been adequately compared, their diagnostic characters have hitherto been uncertain and the stratigraphical value of the individual species has therefore been obscured. The purpose of this paper is to redescribe these species, to establish the facts about their geographical and stratigraphical distributions as accurately as possible, and to indicate the probable evolutionary history of the genus.

Since *Austrotrillina* occurs in both the Tethyan and Indo-Pacific provinces, it is necessary to refer here to two schemes of classification for the Tertiary (Text-fig. 1). Justification for the correlation between part of the East Indian letter stages (Tc–Te) and the European stages may be found in a recent paper (Adams 1965). It is thought wise to retain the two systems until a generally acceptable correlation becomes possible.

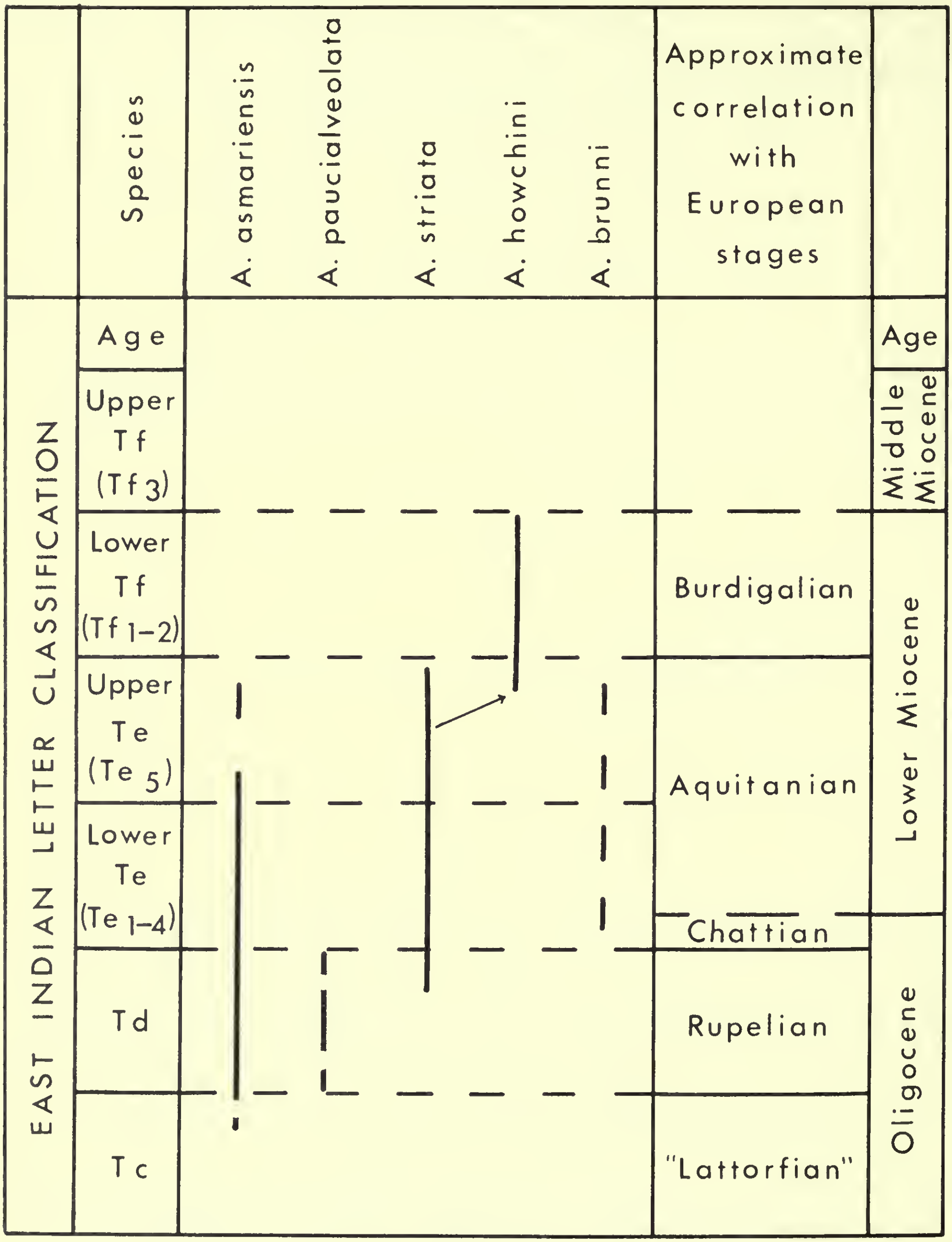

FIG. 1. *Austrotrillina* range chart. Solid lines indicate known ranges; broken lines indicate uncertainty. The European stages are used in the sense of most workers on larger foraminifera up to 1962, i.e. they are based on faunal assemblages rather than on type sections. At the top of its range, i.e. within Lower Tf, *Austrotrillina* overlaps with *Orbulina*.

It was first realized that taxonomic confusion surrounded the species of *Austrotrillina* during a study of the Tertiary faunas of Borneo. At the same time it became clear that the genus showed definite evolutionary changes during the Miocene and that if these could be shown to hold good over the whole of its distributional area, a useful stratigraphical tool would have emerged.

Although well-placed to attempt this study, the writer would have achieved little without the willing co-operation of numerous fellow workers. His special thanks are due to the following: Dr. F. E. Eames (British Petroleum Co. Ltd.) for stimulating discussions, for help in obtaining material from Iran and Malta and for critically reading the manuscript; Dr. T. D. Adams and Mr. J. D. Baignton (Iranian Oil Operating Co.) for additional material from Iran and for much useful stratigraphical data; Dr. R. C. van Bellen and Mr. G. F. Elliott (Iraq Petroleum Co. Ltd.) for the loan of material and for valuable stratigraphical evidence; Dr. N. H. Ludbrook (Department of Mines, Adelaide) for the gift of specimens from the Pata limestone, South Australia, and for much helpful information; Dr. R. Cifelli (U.S. National Museum), Miss Ruth Todd and Dr. N. K. Sachs (U.S. Geological Survey) for making available material in their care. He is also greatly indebted to Dr. F. T. Banner (British Petroleum Company Ltd.), Dr. D. J. Belford (Bureau of Mineral Resources, Canberra), Dr. A. N. Carter (University of New South Wales), Mr. D. J. Carter (Imperial College, London), Professor W. Storrs Cole (Cornell University), Professor M. F. Glaessner (University of Adelaide), Dr. L. Hottinger (University of Basle) and Dr. P. Marie (Paris) for additional information, material, or helpful discussions, Mr. R. L. Hodgkinson provided invaluable technical assistance.

II. STRATIGRAPHICAL NOTES

The species described here were obtained mainly from the successions detailed below. This stratigraphical information is given so that the conclusions regarding stratigraphical ranges and evolutionary history can be evaluated independently by other workers.

1. *The Asmari limestone*

General succession	*Age* (according to Eames *et al.* 1962)
Upper Asmari limestone	Burdigalian
Middle Asmari limestone	Aquitanian
Lower Asmari limestone	Oligocene { upper part Chattian lower part Rupelian

The Asmari limestone overlies the *Brissopsis* beds (Lower Oligocene) in some places; in others it rests disconformably on the Upper Eocene.

Whether or not the middle Asmari limestone is Aquitanian in age seems to be a matter of opinion. Direct correlation with the type Aquitanian is impossible at present, and the published evidence does not appear to disprove an Upper Oligocene age for this part of the sequence.

Material examined in this study consists of:

(a) 2,500 thin sections from wells 6 and 11, Gach Saran Oilfield, Iran. Both wells penetrated all three divisions of the limestone.

(b) The Asmari limestone at Kuh e Pataq, N.W. Luristan (46° 00′ E., 34° 25′ N.). Four samples were available from this locality, here designated as the type section for *A. asmariensis* sp. nov. The microfauna of the whole section has been studied by Dr. T. D. Adams and the ranges of important genera shown on Text-fig. 2 are based on his work. Kuh e Pataq is a surface section on the road from Kermanshah to Baghdad, near the border with Iraq (Text-fig. 2). The lowermost part of this sequence is definitely Eocene, and although it is tempting to regard the oldest Oligocene horizons as Lower Oligocene (occurrence of *Nummulites fichteli* without *Eulepidina*) caution is necessary. *Eulepidina* does not appear until 380 ft. below the top of the limestone and the overlap with *N. fichteli* is small (about 80 ft.). Reticulate nummulites occur through approximately 700 ft. of limestone and overlap with *Chapmanina* (a well-known Eocene genus) throughout their lowermost 130 ft. The writer has not seen these particular specimens and is therefore unable to confirm Dr. T. D. Adams's identification of *N. fichteli* (*in lit.*). It seems reasonable to draw the Eocene/Oligocene boundary at about 845 ft. below the top of the limestone, i.e. at the first appearance of *Austrotrillina*. It may be noted that *Austrotrillina* is not common until after the incoming of *Peneroplis thomasi* about 800 ft. from the top. By 730 ft. *P. thomasi* has already been joined by *P. evolutus* and *Praerhapydionina delicata*. The evidence of this section seems to suggest that *Austrotrillina* occurs in the Lower Oligocene. However, it can equally well be argued that this is a Middle Oligocene fauna from which *Eulepidina* is absent for facies reasons. Pending further investigation of the section—in particular, the detailed examination of the faunas immediately above the Eocene/Oligocene boundary—it would be unjustifiable to state unequivocally that *Austrotrillina* occurs in the Lower Oligocene of Kuh e Pataq, although it certainly occurs in the Middle Oligocene.

(c) The Kuh e Kalagh section (Text-fig. 2). The lowest exposed Oligocene beds in this locality are presumably of Middle Oligocene age (association of *Lepidocyclina*, in part *Eulepidina*, with *Nummulites fichteli*). The base of the Oligocene is obscured and the next visible beds are those of the Eocene Dezak Marl Member. The middle part of the section is either Chattian or Aquitanian but seems to lack diagnostic fossils; the highest levels (above sample JHT 1863 and not shown in Text-fig. 2) can reasonably be assigned to the late Lower Miocene (" Burdigalian ") on the evidence of *Borelis melo curdica*. Ninety-two samples (135 thin sections), collected through 1,138 ft. of rock, have been examined.

2. *The Main Limestone of Kirkuk.*

This limestone is well-known through the work of van Bellen (1956). It has been described from numerous wells which are difficult to correlate owing to the rapidity with which it is said to changes facies both laterally and vertically. The succession

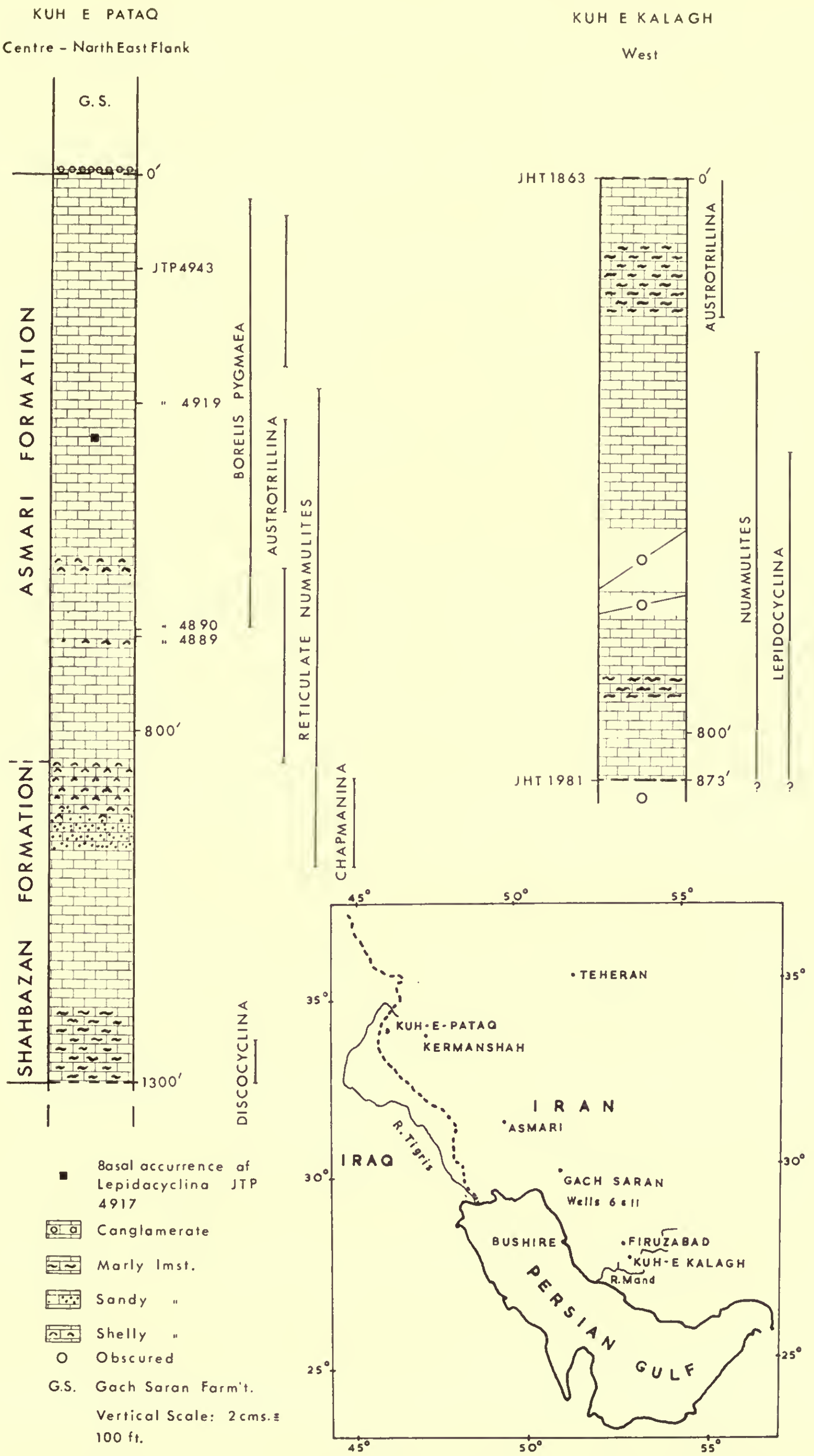
KUH E PATAQ
Centre – North East Flank
G. S.
0′
JTP4943
" 4919
" 4890
" 4889
800′
1300′
ASMARI FORMATION
SHAHBAZAN FORMATION
BORELIS PYGMAEA
AUSTROTRILLINA
RETICULATE NUMMULITES
CHAPMANINA
DISCOCYCLINA
KUH E KALAGH
West
JHT1863
0′
AUSTROTRILLINA
NUMMULITES
LEPIDOCYCLINA
800′
JHT 1981
873′
?
?
Basal occurrence of Lepidocyclina JTP 4917
Conglomerate
Marly lmst.
Sandy "
Shelly "
Obscured
G.S. Gach Saran Farm't.
Vertical Scale: 2 cms. ≡ 100 ft.
45°
50°
55°
35°
30°
25°
TEHERAN
KUH-E-PATAQ
KERMANSHAH
IRAN
ASMARI
IRAQ
R. Tigris
GACH SARAN
Wells 6 & 11
BUSHIRE
FIRUZABAD
KUH-E KALAGH
R. Mand
PERSIAN GULF

FIG. 2. Two surface sections of the Asmari limestone. Kuh e Pataq is the type locality for *A. asmariensis* sp. nov. Data kindly provided by Dr. T. D. Adams (Iranian Oil Operating Companies). For *Borelis pygmaea* read *Borelis pygmaeus*.

in Well K.14, from which *A. paucialveolata* was first described, is as follows:

Succession	*Age*
Lower Fars conglomerate	Burdigalian
———disconformity———	
Baba Formation (Thickness about 30 ft.) (65 ft. in K109, van Bellen p. 260)	Middle Oligocene (on the association of *Nummulites* and *Eulepidina*). Fore-reef.
———disconformity———	
Shurau Formation (Thickness about 30 ft.) (60 ft. in type section, K109; van Bellen p. 260)	High Lower Oligocene or Middle Oligocene. Types of *A. paucialveolata* from here. Back reef.
Sheikh Alas Formation (85 ft. type section; van Bellen p. 260)	Lower Oligocene. *N. fichteli* without *Eulepidina*. Fore reef.

The Bajawan Formation, not represented in Well K14, has as its type locality Well K109 (Baba Dome) where, according to van Bellen, it overlies the Baba limestone conformably, has a thickness of 128 ft. and is developed in "back reef" facies. According to Smout & Eames (1958) the Bajawan Formation is probably Aquitanian in age, but the evidence for this is rather tenuous since it depends largely on the assumption that *Spiroclypeus* does not occur in the Oligocene. It may be noted that van Bellen (1956 : 260) said that the Baba Formation is the fore-reef equivalent of the Bajawan limestone, in which case both are of Middle Oligocene age. On the other hand, van Bellen had not seen *Spiroclypeus* in the Bajawan Formation whereas Smout and Eames had.

3. *Pemba Island*

This sequence was described by Stockley (1927). Morley Davies, who described the Foraminifera in the same publication, recognized the following subdivisions of the Chake-Chake beds which are 100 ft. thick at outcrop.

Upper horizon	*Miogypsina* without *Lepidocyclina*
Middle horizon (Datum Stratum)	*Amphistegina* and *Operculina*
Lower horizon	*Lepidocyclina* with very rare *Miogypsina*

A. howchini was said by Morley Davies to range from "low down to high up" in the Chake-Chake beds. He dated the entire sequence as high Aquitanian or Burdigalian. These beds are here regarded as Lower Tf for reasons which are given later (see p. 88).

4. *The Kirimalai limestone, Ceylon*

This limestone occurs in the northern part of the island on the Jaffna Peninsula. An account of the stratigraphical succession and of the faunas of the Miocene limestones of Ceylon was given by Wayland & Morley Davies (1923). According to these authors, the forminiferal fauna includes *Orbiculina malabarica* (= *Taberina malabarica*), *Sorites* sp., *Alveolinella* (*Flosculinella*) sp. and *Spiroclypeus*? sp. cf. *pleurocentralis*, together with miliolids of various types. They also report the association of *Orbiculina* sp. and *Spiroclypeus orbitoideus* from Minihagalkanda in the south of the island. However, it is not clear whether these species were found in a single sample or whether they occurred at different levels. *A. howchini* and *Taberina malabarica* have been observed together in a thin section of limestone B.M.(N.H.) P22330 from the Wayland collection labelled "North of Pomparippu, N.W. Province, Ceylon."

5. *The Melinau limestone, Sarawak*

The general succession at Melinau is as follows:

Upper Te limestone	1,600 ft.
Lower Te limestone	1,600 ft.
Td limestone	110 ft.
Tc limestone	1,400 ft.
Tb limestone	1,850 ft.

Austrotrillina occurs from highest Td through Te. For full details of this limestone see Adams (1965).

6. *The Pata limestone, South Australia*

This is the youngest Miocene limestone in the Murray Basin, and Ludbrook (1961) has given details of its foraminiferal fauna. She referred it to the highest Burdigalian but, according to Eames *et al.* (1962), its pelagic foraminifera indicate a Lower Burdigalian age. The position of the Pata limestone in terms of the East Indian letter classification is Lower Tf.

7. *The Miocene limestones of Saipan*

Cole (1957) and Hanzawa (1957) have described the foraminifera from large numbers of surface samples collected over the whole island. The geology has been described by Cloud *et al.* (1956). Unfortunately, no good sections were measured and the relative stratigraphical positions of many samples are uncertain from the field evidence. It has been possible to examine the specimens described by Cole (1957) in Washington and Ithaca, and matrix-free individuals have been extracted from two important samples.

8. *The Miocene limestones of Bikini and Eniwetok*

The faunas of these limestones are known only from boreholes, and have been described by Cole (1954; 1958), Todd & Post (1954) and Todd & Low (1960). The types of *A. striata* come from bore 2B on Bikini Island. All the specimens of *Austrotrillina* recovered from these bores have been examined through the courtesy of Miss Ruth Todd and Professor W. Storrs Cole.

9. *The Lower Coralline limestone of Malta*

This limestone is at least 626 ft. thick (House *et al.*, in Bowen-Jones 1961) and is the oldest described rock unit on the island. However, unpublished information (Eames *in. lit.*) shows that this unit is underlain by a miliolid limestone, at least 75 ft. thick, which lacks *Austrotrillina.* The lower Coralline limestone contains, in addition to *Austrotrillina, Peneroplis evolutus, Praerhapydionina delicata, Spiroclypeus blanckenhorni* var. *ornata, Lepidocyclina* (*Eulepidina*) *dilatata, Lepidocyclina* (*Nephrolepidina*) *tournoueri* and *Miogypsinoides complanatus.* On the basis of this assemblage it has been dated as Aquitanian (Eames *in lit.*). Although this is probably correct, it is impossible to be certain on the present evidence that this fauna is not Upper Oligocene in age. As mentioned above, it is often assumed that *Spiroclypeus* does not occur in the Oligocene of the Mediterranean region, but proof is lacking (see Adams 1967).

10. *The Miocene orbitoidal limestones of Christmas Island*

Jones & Chapman (1900) were the first to describe the foraminifera from these limestones. Their material has been re-examined and additional thin sections prepared from some of the original rock samples. Ludbrook (1965) published further valuable information on the faunas and her material has also been examined. Additional collections were made recently by Mr. J. Barrie (Bureau of Mineral Resources, Canberra) and these are now being studied in conjunction with Dr. D. J. Belford.

Ludbrook (1965) dated the uppermost part of the limestone as Tf on the occurrence in one sample (P33) of *Flosculinella bontangensis,* a species generally thought—but never actually proved—to be restricted to strata of Tf age. Upwards of 500 samples have now been collected from the limestones of the island but only in one locality is there any suggestion of an age younger than Te. In this connection it is noteworthy that P33 also contains *Borelis pygmaeus,* a species characteristic of Tc–Te and unknown from Tf. Ludbrook originally stated that *Austrotrillina howchini* occurred in P33 but this proved to be an error. All Ludbrooks' figured specimens of *A. howchini* (*op. cit.*, pl. 21, figs. 4–6) are good examples of *A. striata.*

11. *Eocene limestones of New Caledonia*

Through the courtesy of Professor M. F. Glaessner and Dr. J. Sigal, numerous thin sections of Eocene limestones from New Caledonia in which *Austrotrillina* sp. nov. was thought to occur (see Tissot & Noesmoen 1958), have been examined. These organisms are now known to be different from *Austrotrillina* and are under investigation by Glaessner & Sigal.

III. SYSTEMATIC PALAEONTOLOGY

Family **MILIOLIDAE** Ehrenberg 1839

Genus ***AUSTROTRILLINA*** Parr 1942

Type species *Trillina howchini* Schlumberger 1893.

(a) *Shell structure*

The shell wall is basically simple and may be regarded as consisting of three parts (Text-fig. 3).

1. A solid porcellaneous layer laid down over the outer surface of a previously formed chamber. This was referred to as a " step " by Grimsdale (1952) who considered it to be of taxonomic importance. It is, in fact, inconstant in thickness, both within a species and amongst the specimens from a single assemblage, and is of no taxonomic value.

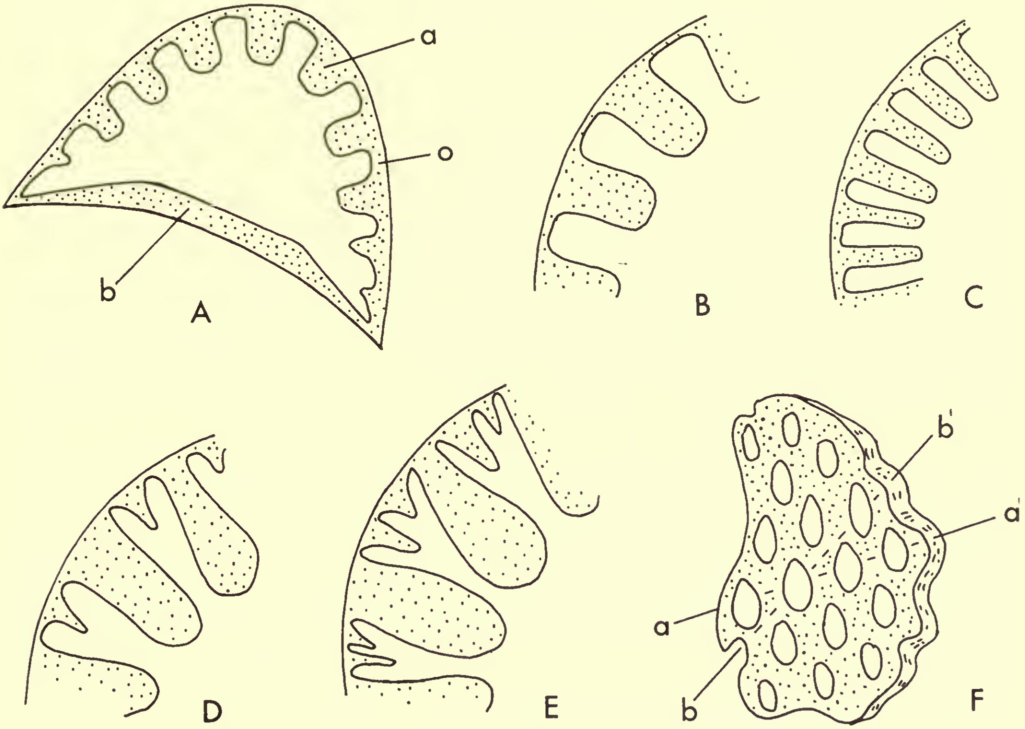

FIG. 3. Wall structure of *Austrotrillina* (drawings all schematic). A. Generalized transverse section through an adult chamber (*a* – alveolar layer; *b* – basal wall or " step "; *o* – outer skin) B. " Striata " type wall with coarse alveoli. C. " Asmariensis " type wall with fine, closely spaced alveoli. D & E. " Howchini " type wall with bifurcating alveoli. E is more advanced than D. F. Wall of *A. striata* seen from inside the chamber. It is clear that the spacing of the alveoli will vary according to the plane of section: a – a′, closely spaced; b – b′, widely spaced. Non-oriented random sections can therefore be misleading. The thickness of the outer skin is greatly exaggerated in these drawings.

2. A curved outer wall consisting of two parts:
   (a) a relatively thick, inner alveolar layer;
   (b) a very thin, non-alveolate, outer skin which is punctate externally.

The outer " skin " being very delicate is lost in most individuals. It can be detected only rarely in specimens seen in thin sections of limestone, and then merely as a dark line.

Alveoli may be fine as in *A. asmariensis* or coarse as in *A. striata*. The apparent diameter of the alveoli varies according to the plane of section. This can be verified by examining the inner surface of the wall (Text-fig. 3F; Pl. 4, fig. 12).

In most specimens of *A. striata* and *A. asmariensis*, and in all the known specimens of *A. paucialveolata*, the alveoli are simple tubes. The extent to which they are present throughout the test seems to be a specific character.

In *A. howchini* the wall structure is more complex in that the alveoli bifurcate and trifurcate towards their outer ends, i.e. towards the exterior of the shell (Text-fig. 3D, E), thus producing a pattern of long and short "septa" when seen in cross section. In primitive forms, bifurcation begins at the chamber angles where the wall is thickest, but in the most highly evolved forms the entire wall is involved.

EMENDED DIAGNOSIS. Test free, calcareous, porcellaneous; external wall consisting of a thick alveolar inner part (except for that portion in contact with a previous chamber) and a thin, finely pitted outer skin: chambers one half coil in length: early chambers—in microspheric generation at least—added in quinqueloculine fashion, later chambers usually arranged in triloculine manner so that only three are visible externally. Aperture probably pseudocribrate.

REMARKS. The alveolar wall and mode of growth are diagnostic for the genus. The wall may be alveolate back to the second chamber, or the alveoli may be confined to the last few chambers. Previous authors have regarded the triloculine arrangement of the chambers as a constant and diagnostic feature, but this is not the case. It is not unusual to find specimens with four chambers visible externally. It should be noted that the figures given in the Treatise on Invertebrate Paleontology (C474, figs 7, 8), although stated to be of the type species, are actually of *A. striata* Todd & Post.

Todd & Post (1954) described the aperture of *A. striata* as cribrate, while Carter (1964) stated that *A. howchini* has a pseudocribrate aperture. The present material does not permit any comment on apertural characters.

The extremely thin outer skin is preserved only under very favourable circumstances.

(b) *Description of species*

Austrotrillina asmariensis sp. nov.

Pl. 1, figs. 1–12.

?1920 *Trillina howchini* Schlumberger; Silvestri: 77, pl. 4, figs 9, 10.
?1929 *Trillina howchini* Schlumberger; Silvestri: 27, pl. 3, fig. 10.
1937 *Trillina howchini* Schlumberger; Silvestri: 81 (pars), pl. 6, fig. 3, ? pl. 5, fig. 3 only.
1947 *Trillina howchini* Schlumberger; Bursch: 12, pl. 1, figs 1, 2, pl. 3, fig. 14. Not text-fig. 3.
1956 *Austrotrillina howchini* (Schlumberger); van Bellen, pl. 1, figs C, D.
?1957 *Austrotrillina howchini* (Schlumberger); Hanzawa: 38 (pars), pl. 22, figs 12, 13. Not pl. 34, figs 1, 2.
?1957 *Austrotrillina howchini* (Schlumberger); Cole: 329, pl. 101, figs 4–6.
1958 *Austrotrillina howchini* (Schlumberger); Smout & Eames: 208.
?1962 *Austrotrillina howchini* (Schlumberger); Dizer, pl. 3, fig. 7.

TYPE LOCALITY: Kuh e Pataq (46° 00 E. 34° 25′ N.) N.W. Luristan, Iran.

TYPE LEVEL: Oligocene (almost certainly M. Oligocene, but above the last nummulites in the section). Sample JTP 4943.

DIAGNOSIS: An *Austrotrillina* with a simple alveolar wall. Alveoli numerous, normally ranging in diameter from 10 to 20 μ.

HOLOTYPE. P47578.

A FORM

DESCRIPTION. Test comprising a globular or subglobular proloculus 0·07–0·25 mm. in internal diameter, followed by nine to fifteen chambers arranged as for the genus. The chamber walls are rounded, and are alveolate except where in contact with a previous chamber. The alveoli are numerous and simple. The walls of the later chambers are usually 50–80 μ in thickness but occasionally reach 110 μ. All chambers after the second have alveolate walls. The nature of the aperture is unknown.

Dimensions of the holotype

Length : unknown
Diameter : 1·10 × 1·78 mm.
Proloculus diameter: 0·2 × 0·18 mm.

Most specimens are relatively short (about 1 mm., few exceed 1·5 mm. in length), and are between 0·5 and 1·0 mm. in diameter. Very compressed specimens, and rare individuals in which the last chamber has been added at 180° to the penultimate chamber, may be wider than this.

Variation. The shape of the test is not constant. Chambers margins are usually bluntly rounded; many specimens are rather flattened or triangular in cross section. Proloculus diameter is very variable, specimens from the Middle Oligocene sometimes having proloculi with a larger internal diameter than that of any other species.

B FORM

This differs from the A form in having more chambers (12–17 or more), a much smaller proloculus, of which no measurements have been obtained, and a thicker wall in the later chambers. The largest specimen so far seen is 2·3 mm. in diameter. The last-formed chambers are more triangular in cross section than are those of the A forms. The wall attains a maximum thickness of about 0·15 mm.

VARIATION: Two specimens show a tendency for the alveoli to bifurcate in the last two chambers.

ASSOCIATED FAUNA: 1. Type level: *Peneroplis evolutus*, *P. thomasi*, *Praerhapydionina delicata*.

2. Lower levels (according to Dr. T. D. Adams): *Archaias asmaricus*, *Borelis*, *Eulepidina*, *Nummulites fichteli*, *Meandropsina anahensis*. The occurrence of *A. asmaricus* and *M. anahensis* so low in the Tertiary requires verification.

REMARKS: This species has frequently been confused with *A. howchini* in the past, and many records of the latter from the Middle and Far East really refer to *A. asmariensis*.

The earliest definite occurrence of the species is in the Asmari Formation at Kuh e Pataq where it occurs in beds which, on the available evidence (see p. 76), can be assigned tentatively to the Lower Oligocene. It occurs commonly in the Middle Oligocene of the same section and in the Shurau Formation of Iraq, which is also M. Oligocene; good specimens have been found in two museum samples from surface exposures in Iran, in each case in association with *Nummulites fichteli*, an indication that these rocks cannot be younger than Middle Oligocene and could be Lower Oligocene in age. Neither sample contained *Lepidocyclina*.

In the Shurau Formation *A. asmariensis* is often associated with *A. paucialveolata*. It occurs abundantly in the Bajawan Formation of Iraq and in derived pebbles in the lower part of the Lower Fars conglomerate: it is common in the middle part of the Asmari limestone.

Silvestri's records from Somalia (1937), said to be from the Oligocene or Miocene are, in part at least, from the Oligocene. Of his illustrated specimens. pl. 5, fig. 2, is a largely recrystallized form which might fairly be assigned to *A. paucialveolata;* pl. 5, fig. 3 is not very clear, but pl. 6, fig. 3 is almost certainly *A. asmariensis*. In no case were these specimens associated with an age-diagnostic fauna, nor were they from successions the ages of which could be determined with certainty.

Records of *A. howchini* (Silvestri 1920, 1929) from the island of Paxos and from Otranto, Apulia, southern Italy, probably refer to this species, although the figures are not really good enough for this to be certain.

Dizer (1962) has recorded *A. howchini*, from beds of supposed Burdigalian age in various parts of N.W. Turkey. Unfortunately, her best illustration is almost indeterminable as details of the wall structure cannot be seen. However, the shape of the chambers strongly suggests that the specimen is *A. asmariensis*. Dizer's other illustration (pl. 1, fig. 16) is unrecognizable owing to poor preservation.

Specimens indistinguishable from *A. asmariensis* are frequently met with in random sections of limestones from the Indo-Pacific where they occur at about the same levels as *A. striata*. They apparently occur in all the known Te limestones of Sarawak and have been seen in the Te limestones along the Kinabatangan River in Sabah and in Te limestones from Saipan (see p. 93). They occur in the Melinau limestone and were referred to the *A. striata/howchini* group by the author (1965).

A. asmariensis differs from typical specimens of *A. paucialveolata* and *A. striata* in having an inner wall that is clearly alveolar back to the third chamber in the A form. It differs from *A. striata* in having more numerous and much smaller alveoli. It differs from *A. howchini* in having simple (i.e. non-bifurcating) alveoli, a thinner wall and a more open chamber lumen in the adult stage (see Table 1).

GEOGRAPHICAL DISTRIBUTION: Middle East, East Africa, south-east Asia, Pacific Islands.

STRATIGRAPHICAL RANGE:? Lower or Middle Oligocene to Lower Miocene in the Tethyan region: Te in the Indo-Pacific region.

Note: Although typical specimens of *A. asmariensis* and *A. striata* (cf. Pl. 1, figs 4, 7, 11, and Pl. 4, figs 11, 4, 13) look very different, the geographical and stratigraphical distributions of the two are such that it is difficult to avoid the conclusion that we are really dealing with one species and that the differences between them are not of fundamental importance. Nevertheless, pending the discovery of matrix-free specimens of *A. asmariensis* and a concomitantly more detailed description, it is advisable to regard it as a distinct species.

Austrotrillina brunni Marie

Pl. 6, figs 6, 8

1955 *Austrotrillina brunni* Marie: 203, pl. 19, figs 4–8.

REMARKS. The only record of this species is from a limestone a few metres thick within " une immense succession gréseuse " to the north-west of the village of Pentafolon in north-west Greece. The limestone was dated as Upper Oligocene or basal Aquitanian on the occurrence of *Miogypsinoides complanatus* (Schlumberger). The only other foraminifera listed from it are *Lepidocyclina* (*Nephrolepidina*) sp., which occurs in abundance, and *Rotalia* sp.

It has not been possible to examine the thin sections in which this species was found, but Dr. P. Marie has kindly made available the original photographs on which the figures on pl. 19 of his paper were based. The reproduction of these photographs in Marie's paper is, unfortunately, not good enough for the internal structure to be clearly discerned. However, the photographs show that the structure of the wall is, in some specimens at least, fairly advanced in type, i.e. the alveoli bifurcate towards their outer ends. On the other hand, in other specimens there is no sign of bifurcation, and these resemble the *A. striata/asmariensis* group. In all specimens the chambers are rounded in cross section and in this respect are unlike the Australian representatives of *A. howchini*. They resemble forms found in Upper Te in the Indo-Pacific region, i.e. they are intermediate between the *A. striata/asmariensis* group and the true *A. howchini*.

On the present evidence it is impossible to assign an accurate age to the Pentafolon limestone. The wall structure of the *Austrotrillina* specimens suggests that the rock is late Aquitanian in age. The presence of *M. complanatus* is not a sufficient indication of age since it ranges from the Oligocene into the early Miocene. Its upper limit does not appear to have been established satisfactorily. Eames (*in lit.*) has indicated that *M. complanatus* is common in late Aquitanian beds in the Middle East; Renz (1936) recorded it from Italy with *Miogypsina irregularis* (Michelotti) (= *M. globulina* (*Michelotti*)) a species usually considered to be " Burdigalian " in age, and Gordon (1961) has reported it from " above the *Orbulina* surface ", i.e. from " Burdigalian " or younger rocks, in Puerto Rico. A further examination of the limestone is necessary to establish whether or not it contains foraminifera that would substantiate an Aquitanian age.

Marie believed that the rounded nature of the chambers and, therefore, of the test, was sufficient to distinguish this species from *A. howchini*. The present author does not share this view. While the youngest Australian representatives of *A. howchini* have triangular chambers, many advanced Tf forms from New Guinea, East Africa and India have rounded chambers. Marie also laid emphasis on the quinqueloculine arrangement of the chambers in *A. brunni*. They are, however, more triloculine than quinqueloculine and are similar to those of *A. striata*, a species which often shows four chambers externally (see Pl. 4, fig. 9).

It is thought that the name *A. brunni* should be retained until such time as oriented sections made from additional material can be compared with sections of other species of the genus.

Austrotrillina howchini (Schlumberger)

Pl. 2, figs 1–7; Pl. 6, figs 1–5, 7

1893 *Trillina howchini* Schlumberger; 119, text-fig. 1, pl. 3, fig. 6.
1908 *Trillina howchini* Schlumberger; Chapman: 753, pl. 39, figs 7–9.
1913 *Trillina howchini* Schlumberger; Chapman: 169, pl. 16, fig. 4.
1927 *Trillina howchini* Schlumberger; Davies: 10, pl. 2, figs 10, 11.
?1927 *Trillina howchini* Schlumberger; van der Vlerk & Umbgrove: 13, text-fig. 2.
1936 *Trillina howchini* Schlumberger; Renz: 32, pl. 15, figs 4, 5.
1936 *Trillina howchini* Schlumberger; Crespin: 6, pl. 1, figs 1, 2.
1941 *Trillina howchini* Schlumberger; Rao: 7, pl. 2, fig. 7.
1942 *Austrotrillina howchini* (Schlumberger); Parr: 361–2, figs 1–3.
1954 *Austrotrillina howchini* (Schlumberger); Crespin: 40, pl. 7, fig. 14.
1955 *Austrotrillina howchini* (Schlumberger); Crespin: 60–1, pl. 9, fig. 4.
?1957 *Austrotrillina howchini* (Schlumberger); Hanzawa: 38 (pars), pl. 34, figs. 1, 2. Not pl. 22, figs 12, 13.
1962 *Austrotrillina howchini* (Schlumberger); Eames *et al.*, pl. 6, figs B, E.
1964 *Austrotrillina howchini* (Schlumberger); Carter: 62, pl. 1, figs 12–17.

DIAGNOSIS. An *Austrotrillina* with a smooth, finely pitted test; wall thick, with closely spaced alveoli which bifurcate—sometimes more than once—towards their inner ends to form secondary and tertiary alveoli.

A FORM

DESCRIPTION. Test comprising a subglobular proloculus (0·07–0·15 mm. in diameter) followed by a tube-like second chamber; subsequent chambers arranged in a triloculine manner so that not more than three are visible externally. The shell normally consists of from ten to twelve chambers (proloculus excluded). The non-alveolar outer skin is very thin (5–10 μ) and is covered with fine, shallow pits. The inner layer is thick, alveolate, the alveoli bifurcating as they approach the outer skin so that primary, secondary and tertiary alveoli appear. The dividing walls between the secondary and tertiary alveoli are always much shorter than the primary dividing walls and thus appear as short " septa " in transverse sections. The alveoli make a sharp turn as they reach the outer skin and end blindly (Pl. 2, fig. 6). Transverse sections cut through the upturned ends of the alveoli produce the impression of vertical canals (Pl. 2, fig. 3). The alveolar layer is always thickest at the chamber angles; it often occludes much of the chamber lumen. The aperture is pseudocribrate according to Carter (1964).

B FORM

Only one specimen available.

Similar to the A form but with a much smaller proloculus. Test composed of at least sixteen chambers.

Measurements: length: not recorded, but not noticeably greater than that of the A form

diameter: 2·14 × 1·35 mm.
wall thickness: 0·17–0·35 mm.

Variation: In most specimens, especially those from Australia, the chambers are triangular in shape rather than rounded.

Remarks. Schlumberger described the A form of this species from Muddy Creek, Hamilton, Victoria, southern Australia, and the B form from the Philippines. However, in the absence of an adequate figure and description of the latter form there is no certainty that he was describing the same species. Carter (personal communication) has recently confirmed that it is impossible to tell either the exact locality or the horizon from which Schlumberger's Australian specimens came. The only beds in Victoria from which matrix-free specimens can now be obtained are poorly exposed at Gippsland.

Most of the specimens described here come from the Pata limestone, penetrated in a boring at the Chowilla Dam Site, River Murray, South Australia. Ludbrook (1961; 1963) assigned this limestone to the uppermost Burdigalian on the ground that it contained *A. howchini* together with *Orbulina universa*. It is thus approximately that same age as the Trealla limestone in West Australia. Ludbrook (1963) also notes that *A. howchini* occurs with *Flosculinella bontangensis* (Rutten) and *Marginopora vertebralis* Blainville (the former is a typical Lower Tf or " Burdigalian " species) in the Nullarbor limestone of the Eucla Basin, South Australia.

A. howchini has been recorded fairly frequently from the Miocene of Australia and is known from the Cape Peninsula in the west (Crespin 1955) to Victoria in the south. It occurs in beds of Lower Tf age in the Tulki and Trealla limestones of west Australia. In the Trealla limestone it is associated with *Orbulina universa* as well as with numerous other Tf marker fossils. In Victoria (Carter 1964) it appears two zones below *Orbulina universa* and *O. suturalis* and gives its name to a zone.

Most records of *A. howchini* from outside Australia are, unfortunately, incorrect. The only occurrences known to the writer that can be properly substantiated are as follows.

1. *Lower Miocene limestones of the Malabar coast. Cochin, Travancore, India.* In these limestones *A. howchini* occurs together with *Taberina malabarica*. These beds were said by Carter (1853) to be Pliocene in age, but the foraminifera prove otherwise. Carter did not mention *A. howchini*, but it is a common species in his samples (see pl. 6, figs 2, 4, 5). It also occurs in Miocene conglomerates in the Tapti area, western India (Rao 1941).

2. In the Lower Miocene limestones of Ceylon, *A. howchini* occurs with *Taberina malabarica*. Wayland & Davies (1923) also reported *Flosculinella* and *Spiroclypeus* from these limestones. The latter genus was stated to be represented by two speci-

mens. It does not occur in any of the three slides deposited in the British Museum (Natural History), neither has it been found in additional samples recently examined. Its occurrence in this limestone is therefore open to doubt. The specimens referred by Davies to *Flosculinella* are very poorly preserved and may or may not belong to this genus. The evolutionary stage reached by the wall structure of the *Austrotrillina* specimens from these samples allows the rock to be dated as Lower Tf or " Burdigalian ". *Flosculinella* commonly occurs in strata of this age whereas *Spiroclypeus* does not.

3. *Lower Miocene limestones of East Africa: A. howchini* occurs with *T. malabarica, Miogypsina thecidaeformis* and *Miogypsinoides dehaarti* in the Lower Chake beds of Pemba Island, and with *T. malabarica* in beds of a similar age in the Hadu-Fundi Isi area of Kenya. Following the recent discovery of *Flosculinella bontangensis* in the Chake Chake beds (Eames *et al.* 1962) these can be regarded as Lower Tf in age. *F. bontangensis* alone, cannot as yet be considered as diagnostic of Tf, but in the light of the evidence presented in this paper its occurrence with *A. howchini* s. s. does constitute a satisfactory indication of age.

4. *The Melinau limestone, Sarawak:* In the uppermost part of this limestone (Upper Te) specimens transitional from *A. asmariensis* to *A. howchini* occur (Pl. 5, figs 1, 4). Planktonic foraminifera, including *Praeorbulina* cf. *glomerosa* (Blow), occurring in samples collected in 1966 from the highest beds in the Terikan River, indicate that the top of the limestone is in Zone N8 of Banner & Blow (1965) and not in the *C. dissimilis* Zone as previously suggested (Adams 1965). Primitive representatives of *A. howchini* have also been seen in bore-hole material from the Suai Baram area, Sarawak.

5. *Saipan:* A problem arises in connection with the fauna of the Tagpochau limestone. Cole (1957) regarded this limestone as Te in age while Hanzawa (1957) thought that at least part of it was Tf. Hanzawa (1957, table 2, sample g; table 4, sample 3) reported *Spiroclypeus tidoenganensis* and *Orbulina universa* as occurring together in samples from Saipan and Tinian. However, an examination of the very numerous Miocene samples from Saipan deposited in the U.S. National Museum has failed to reveal *Orbulina* in association with *Spiroclypeus*. Reasonable doubt therefore exists about the accuracy of some of Hanzawa's determinations of one or other of these genera. Both *A. striata* and *A. howchini* occur on Saipan. The former species is the more common, the latter occurring only in a small number of samples (e.g. B413).

Although the common species in Saipan is *A. striata*, specimens indistinguishable from *A. asmariensis* are sometimes seen in random thin sections. This is also true of the Bornean limestones. Whether this means that *A. asmariensis* and *A. striata* are really synonymous, or that the range of variation of some characters overlaps is not clear. However, when total assemblages are considered there is no difficulty in deciding which species is present.

6. *Pacific Isles:* Todd & Low (1960) stated that *A. howchini* occurred in the upper part (1100–1110 ft.) of Eniwetok drill hole E–1 and from 560–570 ft. in F–1.

These authors kindly allowed the writer to examine and section the specimens on which their identification was based. This study showed that the two lowest specimens should have been referred to *A. striata* and the highest to " miliolid *gen.* et *sp.* indet." Similarly, the specimens described as *A. howchini* by Todd & Post (1954) from Bikini are also incorrectly identified. It should be said that these identifications were based on the external appearance of the tests, all of which were decorticated. We now know that external appearances can be misleading, but this was not known when the Bikini and Eniwetok bores were first examined. It can therefore be stated that no specimens of *A. howchini* are known from the Pacific Isles east of Saipan although it is probably only a matter of time before they are discovered.

Most records of *A. howchini* from the Far East are impossible to verify as they are unaccompanied by figures. However, it is probable that all records of *A. howchini* from beds of Tf age can be accepted as correct, except where the dating depends on the presence of *Austrotrillina*. This is certainly true of New Guinea where excellent examples of *A. howchini* occur in Tf limestones. Records from beds of Upper Te age cannot be accepted at their face value unless accompanied by figures: records from beds of Td and Lower Te age are almost certainly incorrect, and in all probability refer either to *A. asmariensis* or to *A. striata*.

7. *Europe and the Middle East:* The only definite record of *A. howchini* from Europe appears to be that of Renz (1936) who reported it from the Burdigalian of the central Apennines. His specimens have been examined. *Austrotrillina brunni*, from the Lower Miocene of Greece is not, of course, far removed from *A. howchini* and is very probably a transition form from *A. striata* (see below). The specimens illustrated by Silvestri (1920, 1929) seem to have a simpler wall structure than *A. howchini s. s.* Hottinger's record (1963) of this species from the Oligocene of Spain is really of *A. paucialveolata*.

Dizer's record (1962) of *A. howchini* from the Miocene of the Sivas Basin, Turkey, is almost certainly incorrect as was indicated earlier (p. 84).

Stefanini's record (1921 : 124) of *A. howchini* from the Oligocene of Cyrenaica is unacceptable as his figured specimen is not even recognizable as *Austrotrillina*. The writer has, however, seen specimens of the *A. striata/asmariensis* type from early Miocene deposits of Libya.

GEOGRAPHICAL DISTRIBUTION: Known from Europe, East Africa, India, Indonesia, New Guinea, Saipan and Australia.

STRATIGRAPHICAL DISTRIBUTION: Mainly Lower Tf (= " Burdigalian " of Europe). Transitional forms from *A. striata* and *A. asmariensis* occur in Upper Te beds of south-east Asia and Saipan.

Austrotrillina paucialveolata Grimsdale

Pl. 3, figs 1–6

?1937 *Trillina howchini* Schlumberger; Silvestri (pars): 81, pl. 5, fig. 2.
1952 *Austrotrillina paucialveolata* Grimsdale: 229, pl. 20, figs. 7–10.
1956 *Austrotrillina paucialveolata* Grimsdale; van Bellen, pl. 3, fig. A, pl. 6, fig. B.

?1962 *Austrotrillina paucialveolata* Grimsdale; Dizer: 43–4, pl. 2, figs 1, 2.
1963 *Austrotrillina howchini* (Schlumberger); Hottinger: 964, pl. 1, figs 1, 2.

EMENDED DIAGNOSIS. An *Austrotrillina* with simple alveoli restricted to the last few chambers.

A FORM

DESCRIPTION. Test comprising a proloculus, a tube-like second chamber and up to fourteen further chambers arranged roughly in a triloculine fashion. The alveoli are simple and appear to be confined to the last four to six chambers. The diameter of the proloculus ranges from 0·08 to 0·13 mm. in the few specimens measured. The nature of the aperture and the surface appearance of the test are unknown.

B FORM

Only a few off-centre sections available. Larger than the A form, and presumably with more chambers. Maximum number of chambers observed is thirteen. Wall up to 0·15 mm. thick. Maximum observed diameter 2·15 mm.

REMARKS. The original description of this species is extremely short and has not previously been emended. Grimsdale only stated that the alveoli were coarser than in *A. howchini.* However, the specimens he had in mind when making this comparison were not *A. howchini s. s.* but *A. asmariensis* sp. nov. as is shown below. After examining Grimsdale's syntypes, specimens from the Iraq Petroleum Company's collections in London, and large numbers of thin sections from the Asmari limestone in the Gach Saran oilfield (Gach Saran wells 6 and 11) and from Kuh e Pataq and Kuh e Kalagh, the following conclusions have been reached:

1. All the specimens of *A. paucialveolata* so far described from the type area are poorly preserved, and the apparent coarseness and irregularity of the alveoli is due in all cases to poor preservation caused by recrystallization of the limestone and of the shell walls.
2. Grimsdale's specimens included both A and B forms although he appears to have been unaware of this. The two largest figured syntypes were probably both B forms.
3. The " step " described by Grimsdale is a thickening of the basal wall. It is not a constant character but varies in development amongst specimens from the same population. It is very prominent in some individuals of *A. striata* (Pl. 4, fig. 13) and *A. howchini* (Pl. 2, fig. 3), and occurs to some extent in all representatives of the genus.
4. *A. paucialveolata* occurs with *A. asmariensis* (= *A. howchini sensu* Grimsdale and van Bellen) in the Lower Asmari limestone.
5. The only diagnostic features of this species seem to be the restriction of the alveoli to the last few chambers, coupled with the fact that the walls of the early chambers appear to be thick. These features could, however, be recrystallization effects.

6. There is no evidence as yet that *A. paucialveolata* occurs at stratigraphically lower levels than *A. asmariensis*. However, since it has not so far been reported above the Middle Oligocene it is worth regarding as separate from *A. asmariensis* for the present.

If future work on isolated, matrix-free specimens shows conclusively that *A. paucialveolata* and *A. asmariensis* are synonymous, then the former name will have priority regardless of the fact that it will be inappropriate descriptively.

Grimsdale (1952) described this species from the Miliola limestone of the Kirkuk oilfield, Iraq, stating in his plate explanation that the syntypes came from Kirkuk Well no. 14. No depth or horizon was given. The age was stated to be Oligocene, but from the information given in his text (p. 224) it is impossible to deduce whether it is Lower, Middle or Upper Oligocene. Although not specifically stated, the implication is that the Miliola limestone is younger than Lower Oligocene since it rests on beds of undoubted Lower Oligocene age.

Van Bellen (1956) described Kirkuk Well 14 in detail, and figured additional specimens of *A. paucialveolata*. Examination of van Bellen's plate revealed that among the ten specimens figured were the three original syntypes of Grimsdale. Van Bellen was apparently unaware of this as he made no mention of it in the text. This refiguring is extremely fortunate since it fixes the exact horizon of the types as 34 feet below the Lower Fars Conglomerate, i.e. in the Shurau Formation. This Formation in Kirkuk Well 14 is only thin, 30 ft. at most, whereas in the type section (Well K109) it is 60 ft. thick. From van Bellen's paper it seems probable that the Shurau Formation is of late Lower Oligocene age, since it conformably overlies the Sheikh Alas Formation of undoubted Lower Oligocene age (contains *Nummulites fichteli* without *Eulepidina*) and is itself disconformably overlain by the Baba Formation—presumably Middle Oligocene in age since it contains both *N. fichteli* and *Lepidocyclina* spp.

Silvestri's (1937) record of this species was discussed by Grimsdale (1952) and nothing further can be added here. The only other record from the Middle East seems to be that of Dizer (1962). Her figures are obviously of poorly-preserved specimens and she gives no description.

It is significant that the material described by Grimsdale and van Bellen came from the same well, and it is even more significant that van Bellen recorded *A. howchini* (really *A. asmariensis* sp. nov. or *A. striata*) from the same level in this well. In correspondence, Dr van Bellen has confirmed that *A. paucialveolata* and the species he called *A. howchini* are known in association in at least two other wells.

The only reliable record of *A. paucialveolata* from outside the Middle East is that of Hottinger (1963) who recorded it as *A. howchini* from the Oligocene of Spain. Hottinger's specimens have been examined and two of them are figured here (Pl. 3, figs 5, 6).

GEOGRAPHICAL DISTRIBUTION: Iraq, Iran, Spain, Turkey.

STRATIGRAPHICAL RANGE: Only known with certainty from the highest part of the ? Lower Oligocene or from the Middle Oligocene of the Middle East, and from the Oligocene (? Middle Oligocene) of Spain.

Austrotrillina striata Todd & Post

Pl. 4, figs 1–13 ; Pl. 6, fig. 9

1954 *Austrotrillina striata* Todd & Post: 555, pl. 198, fig. 9.
1954 *Austrotrillina howchini* (Schlumberger); Cole: 573, pl. 210, figs. 6–9.
1960 *Austrotrillina striata* Todd & Post; Todd & Low: 825, pl. 261, fig. 22.
1965 *Austrotrillina howchini* (Schlumberger); Ludbrook: 292, pl. 21, figs. 4–6.

DIAGNOSIS: A species of *Austrotrillina* distinguished by its simple, coarse alveoli and finely striate surface.

A FORM

DESCRIPTION: Test comprising a spherical proloculus (0·05–0·13 mm. in diameter) followed by up to sixteen chambers arranged in a quinqueloculine fashion. The inner layer of the wall is thick and does not become markedly alveolate until the fifth or sixth chamber. The alveoli are mainly simple and are coarse. Their apparent width, seen in thin section, depends on the plane through which the wall is cut (see Text-fig. 3 F, pl. 4, fig. 12). The lumen of the chambers remains open throughout the adult stage. The outer, non-alveolate, skin is very thin (10–15 μ), finely pitted, and ornamented by fine striae which tend to become coarser on the apices of the external margins. Wall thickness ranges from 0·06–0·11 mm. (usually 0·06–0·08 mm.). The chambers are rounded in transverse section. Many topotype specimens are only weakly striate, a few are possibly non-striate. Aperture cribrate according to Todd & Post (1954).

B FORM

Pl. 5, fig. 9, (not from type area).

DIAMETER: 1·28 × 0·78 mm.

WALL THICKNESS: 0·08–0·18 mm.

PROLOCULUS DIAMETER: 0·025 mm. Nineteen chambers visible.

REMARKS: The original figures of this species are somewhat misleading in that they show only a few relatively coarse striae in the centre of the test. Inspection of numerous topotypes has shown that in typical specimens the whole wall is very finely striate (Pl. 4, fig. 9). This species was originally said to differ from *A. howchini* in its striated surface, much coarser textured alveoli, and in being less distinctly triangular in transverse section. No thin section showing the wall structure was figured. Cole (1954), in a companion publication in the same volume, figured thin sections of a form he called *A. howchini* from the same levels in the Bikini drill hole as the types of *A. striata*. These specimens have been examined and there is no doubt that most of them are examples of *A. striata*.

As mentioned earlier, Cole's figures were, unfortunately, reproduced in good faith by Loeblich & Tappan as *A. howchini*. It should be noted that the surface striae do not show up in thin sections. The alveoli in Cole's specimens are very like those seen in some individuals of *A. asmariensis*. In a few specimens there is a tendency for the alveoli to bifurcate (Pl. 3, fig. 9), but this is not pronounced or common. Such individuals are intermediate between *A. striata* and *A. howchini.*

GEOGRAPHICAL DISTRIBUTION: The Pacific Isles, Indonesia, Christmas Island, i.e. Indo-Pacific. Perhaps also the Tethyan region. Specimens seen by the writer from the Lower Coralline limestone of Malta (Pl. 3 fig. 7) are best referred to as *A.* cf. *striata* for the time being.

STRATIGRAPHICAL RANGE: Uppermost Td and throughout Te in the Indo-Pacific. Uncertain in the Tethyan region, but probably Upper Oligocene and lowermost Miocene (Aquitanian).

Limestones of Upper Te age in Borneo, Saipan and Christmas Island all contain *Austrotrillina* specimens that are morphologically intermediate between *A. striata* and *A. howchini.* True specimens of *A. striata* always occur in the same populations. There can be no doubt that *A. howchini* evolved from *A. striata* in Upper Te times.

(c) *Outstanding problems*

1. Detailed descriptions of *A. asmariensis, A. paucialveolata* and *A. brunni* based on matrix-free specimens are necessary. Until these become available it will be impossible to decide the exact relationships of these species to each other and to *A. striata.*

2. More precise information is needed on the ranges of all the species. In particular, it would be interesting to know whether or not *A. asmariensis* and *A. paucialveolata* occur in undoubted Lower Oligocene beds outside the Middle East.

IV. CONCLUSIONS

On present evidence it is possible to recognize five species of *Austrotrillina* in rocks of ? Lower or Middle Oligocene to Lower Miocene age. The type species, *A. howchini,* has a more complex wall structure than the others and represents the end point in the evolution of the genus. Two species, *A. brunni* and *A. paucialveolata,* are poorly known and of uncertain stratigraphical value. The others are extremely useful for correlation.

The most important characters for species differentiation are (a) the structure of the inner wall and (b) the type of surface ornament. In all other respects the tests are remarkably similar, a fact that may be taken to indicate a monophyletic origin for the genus. There seem to be no significant differences in the size of test, diameter of the proloculus or number or arrangement of chambers between the species. The distinguishing characters for the various species are set out in Table 1.

The identification of species of *Austrotrillina* is a relatively simple matter provided that preservation is reasonably good and that oriented sections, or a sufficient number of random sections, are available. It is, however, dangerous to try to distinguish between *A. asmariensis, A. paucialveolata* and *A. striata* on badly preserved material or on rare random sections in limestones. Members of the Miliolidae are amongst the first foraminifera to be affected by recrystallization, and *Austrotrillina,* because of its alveolar wall, is particularly prone to partial destruction.

TABLE I

Key for identification of species of *Austrotrillina*—A forms only.
Data on size of test, proloculus diameter, number of chambers, not included as no significant differences were observed.

	A. asmariensis	*A. brunni*	*A howchini*	*A. paucialveolata*	*A. striata*
Ornament	smooth ?	?	smooth, but surface finely pitted: sub-surface reticulum visible when wet.	smooth ?	finely striate and finely pitted.
Alveoli	simple; closely spaced	simple or bifurcating	birfurcating; often very complex	simple; irregular ? or like *striata*	simple; widely spaced.
Extent of alveolar layer	throughout test	uncertain: probably throughout test	throughout test	restricted to last few chambers	probably throughout test but usually not seen in early chambers
Number of alveoli/100 μ Measured in oriented cross sections	3 or more	——	——	irregular ?	2–3
Total thickness of wall in adults	usually 50–80 μ; rarely up to 110 μ.	thick	thick: 70–290 μ often 200 μ or more at chamber angles	60–70 μ	60–110 μ
Thickness of outer skin	thin: about 10 μ	?	5–8 μ	?	10–15 μ
Chamber lumen	open	open	much reduced	open	open
Cross-sectional appearance of chambers	rounded	rounded	triangular or rounded	rounded or bluntly triangular	rounded

Austrotrillina appeared in the Oligocene of the Middle East, its first recorded occurrence being with *Nummulites fichteli*. The earliest known forms can be assigned to *A. asmariensis*. In the Shurau Formation of Iraq, *A. asmariensis* occurs alongside *A. paucialveolata*. The latter species does not appear to have achieved a wide geographical or stratigraphical distribution; it is based on recrystallized or otherwise badly preserved specimens and may eventually prove to be synonymous with *A. asmariensis* or *A. striata*.

A. asmariensis persisted virtually unchanged from the Middle Oligocene into the Lower Miocene (Aquitanian). In the Indo-Pacific, *A. striata* appeared in late Td times and persisted through Te. It is possible that these are two forms of the same species.

Present evidence indicates that the transition from *A. striata* to *A. howchini* began in Upper Te times in the Indo-Pacific and that this process was complete by Tf times. In Lower Tf times (" Burdigalian " in the Tethyan region) all known representatives of the genus were of the advanced *A. howchini* type. This last species was widely distributed, ranging from the western Tethys to Australia.

The writer believes that all the species of *Austrotrillina* belong to a single lineage and that, in a sense, they all belong to one species. The evolutionary changes shown by the test will allow us to delimit a number of " species " which are of value stratigraphically. These specific names should be maintained for as long as they can be shown to be of stratigraphical value.

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PLATE 1

Austrotrillina asmariensis sp. nov.

All × 50 approximately

FIG. 1. B form, P39430. Kirkuk Well 56. Henson colln.

FIG. 2. A form, P43667. Bajawan limestone, Kirkuk. Smout & Eames colln.

FIG. 3. A form, P39647. Kirkuk Well 56, Henson colln. (Figs. 2, 3 = *A. howchini sensu* Smout & Eames 1958).

FIG. 4. Off-centre, axial section, P47579. Sample J.T.P.4943, Kuh e Pataq, Luristan. Oligocene.

FIG. 5. Holotype, P47578. Sample J.T.P.4943, Kuh e Pataq, Luristan, Oligocene.

FIG. 6. Off-centre, transve rsesection, P47580. Sample J.T.P.4890 Kuh e Pataq, Middle Oligocene.

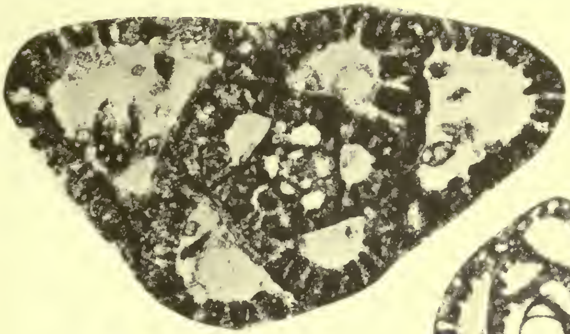
FIG. 7. A form, P47581. Kirkuk Well K93, core 2, 2655 ft. 3 in. Ex. I.P.C. colln.

FIG. 8. A form, P47582. Gach Saran Well 6, 4132–33 ft. Asmari limestone, Iran.

FIGS. 9, 10. A forms, P47583. Kirkuk Well K14, 2793–2808 ft. Ex. I.P.C. colln.

FIG. 11. A form, P47584. Kirkuk Well K93, core 2, 2655 ft. 3 in. Ex. I.P.C. colln.

FIG. 12. B form. P47585. Gach Saran Well 6, 4135–36 ft., Asmari limestone, Iran.



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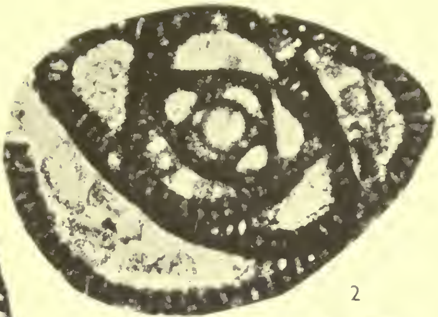

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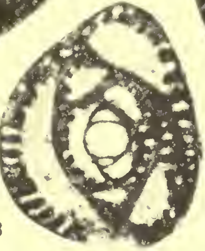

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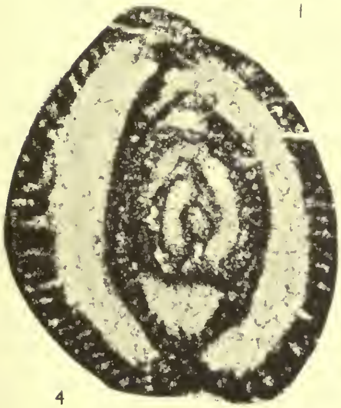

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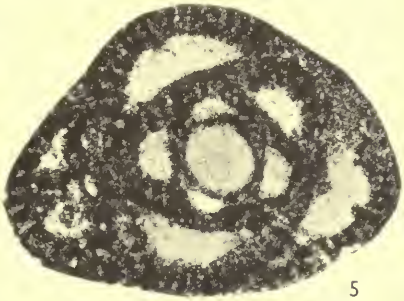

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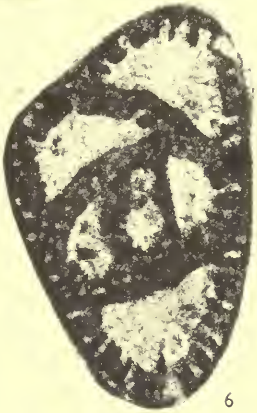

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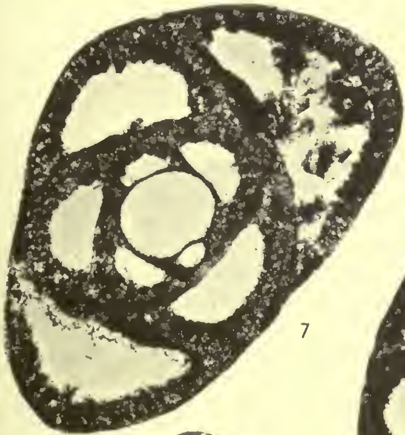

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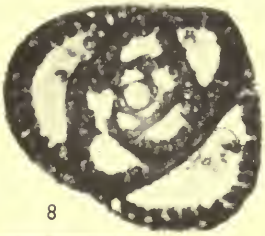

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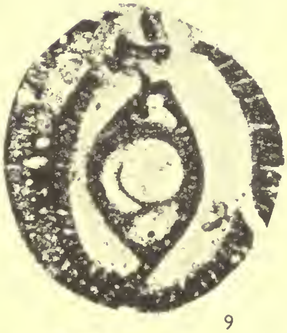

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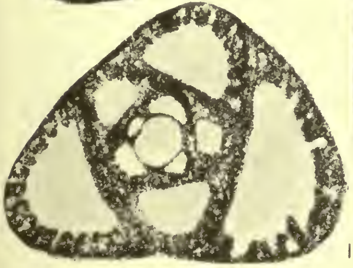

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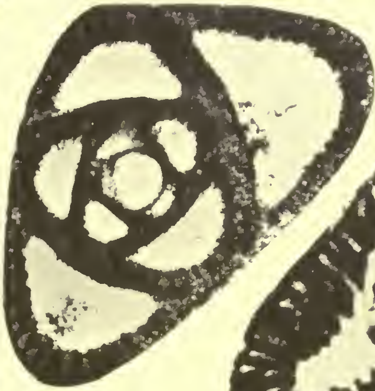

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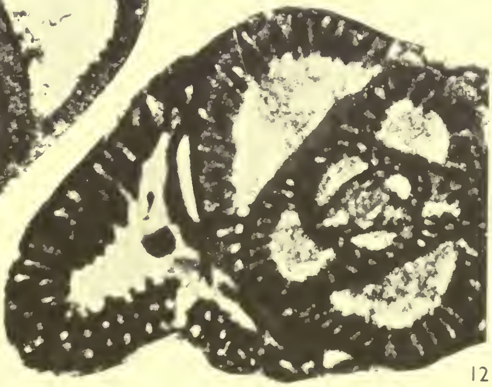

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PLATE 2

Austrotrillina howchini (Schlumberger)

All from the Pata limestone- drill hole P.Q. 2, 273–75 ft., Chowilla Dam site, South Australia. Lower Miocene (Bairnsdalian). Ex. Geol. Surv. S. Australia collections.

Figs. 1, 2. P47586. (1) External view of test × 35 ; (2) portion of wall more highly magnified showing finely pitted outer surface and sub-surface reticulation. See also Pl. 6, fig. 7.

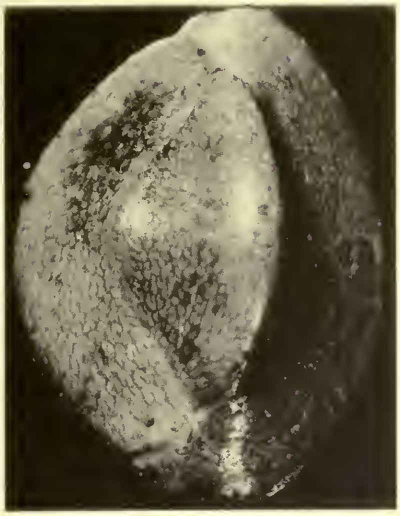
Fig. 3. Transverse section of A form, × 48, P47587.

Fig. 4. Transverse section of a more inflated A form, × 50, P47588.

Figs. 5, 7. Decorticated A form, P47590 (cf. Fig. 1). Most specimens of *Austrotrillina* are found in this condition : (5) × 35 : (7) same specimen × 50.

Fig. 6. A form, P47589. Axial section of a specimen which closely resembled fig. 1 externally.

For B form see Plate 6.



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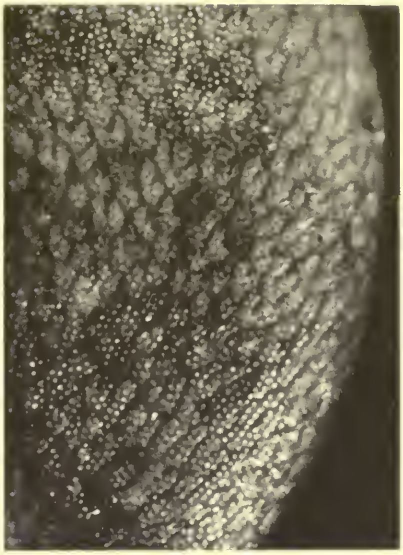

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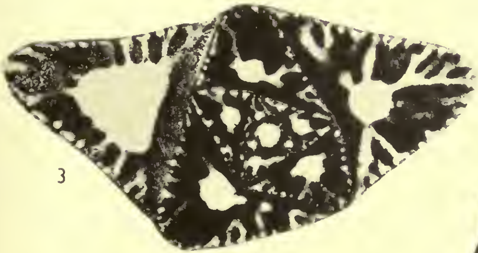

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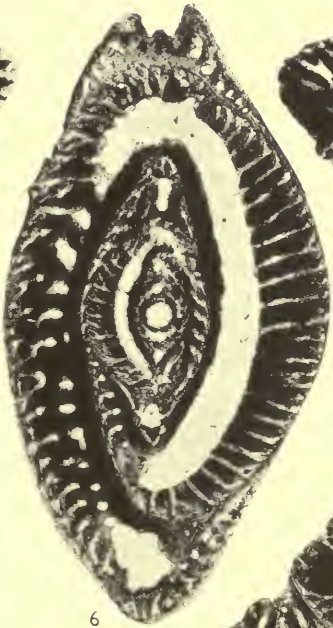

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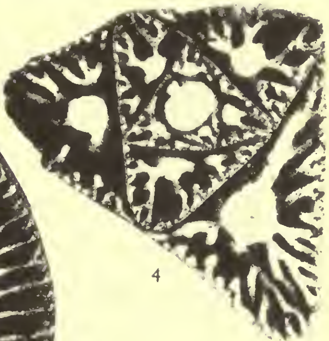

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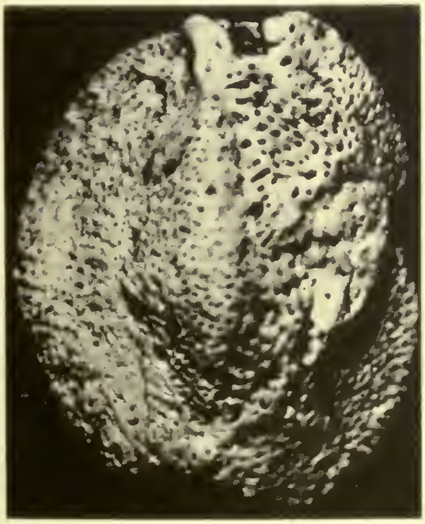

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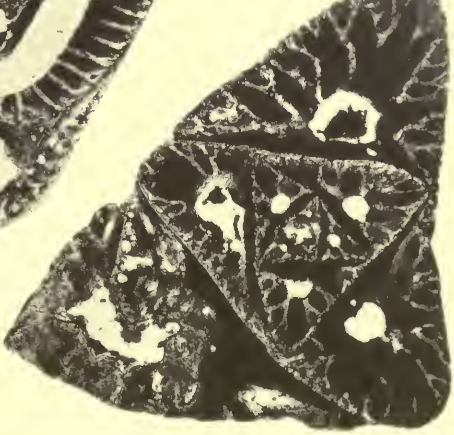

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PLATE 3

FIG. 1. ***Austrotrillina paucialveolata.*** Syntype ×48, P40681; Kirkuk Well No. 14, Oligocene. Probably a B form.

FIG. 2. ***A. paucialveolata.*** A form, ×50, P47591; Kirkuk Well 14, 2828–53 ft., Oligocene.

FIG. 3. ***A. paucialveolata.*** A form, ×50, P40344; Kirkuk Well 14, 2828–53 ft., Oligocene.

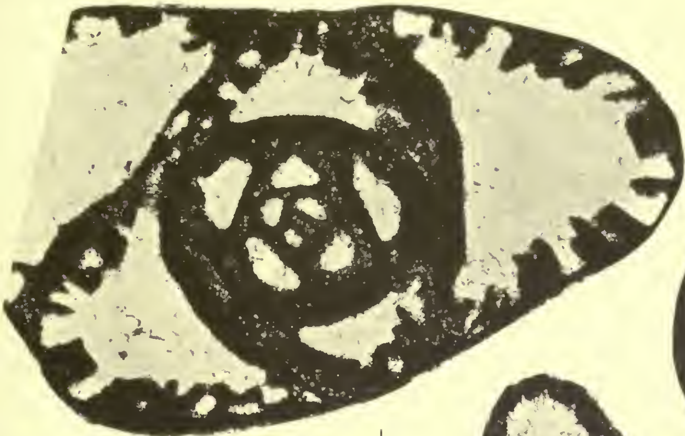
FIG. 4. A form, ×50, P40681 (syntype): Kirkuk Well 14.

FIGS. 5, 6. ***A. paucialveolata.*** A form, Oligocene of Moratalla, Spain (= *A. howchini* of Hottinger 1963) (5) ×55; (6) ×50. Deposited in the Naturhistorisches Museum collections, Basle.

FIG. 7. ***A.*** cf. ***striata*** ×50. Lower Coralline limestone, Malta, Brt. Petrol. Co., Colln.

FIG. 8. ***A. striata,*** ×50. Wall partly destroyed by recrystallization. This specimen is indistinguishable from *A. paucialveolata* and is only determinable as *A. striata* from associated individuals. Tagpochau limestone, Saipan. U.S.G.S. colln., sample No. MSB 260.

FIG. 9. ***A. striata/howchini*** ×50. Bikini drill hole 2B 2038½–48 ft. This is one of the specimens figured by Cole (1954) as *A. howchini* and refigured in the *Treatise* (1964, fig. 362–8) under the same name. It is, in fact, intermediate between *A. howchini* and *A. striata*. U.S.N.M. Colln.



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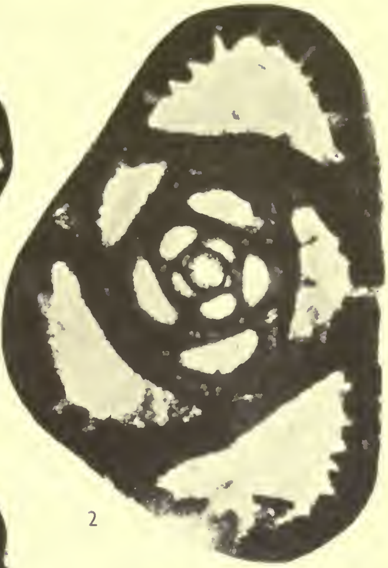

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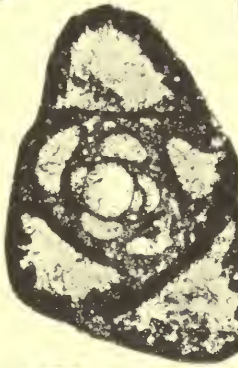

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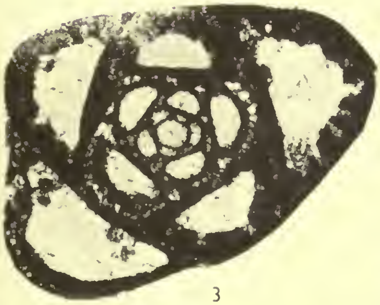

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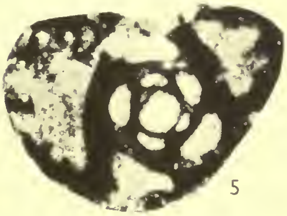

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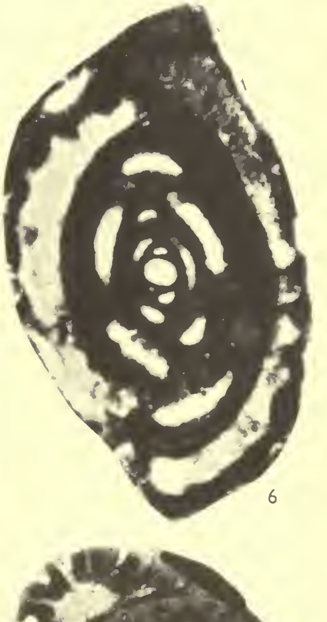

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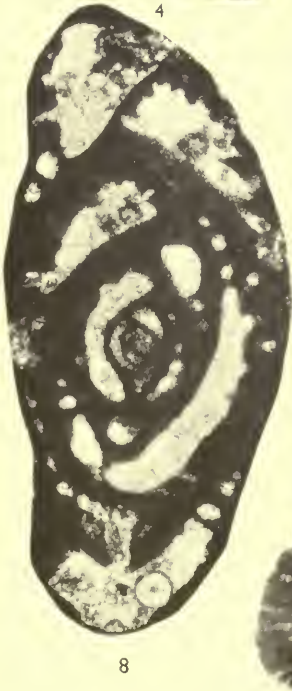

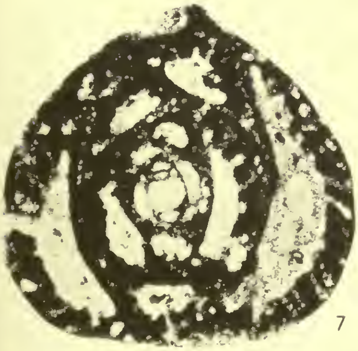

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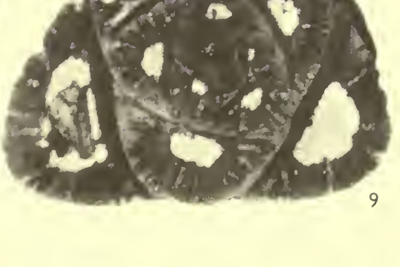

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PLATE 4

Austrotrillina striata Todd & Post

All × 50 unless otherwise stated

FIGS. 1–3. A forms (P47592, P47593) from Eniwetok drill hole E-1, 1895–925 ft. Figs. 1, 2 are of the same individual. Fig. 2 shows the external appearance of the test when immersed in oil; decorticated specimens also look like this.

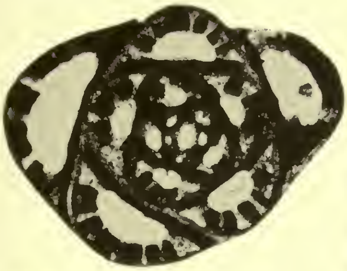
FIGS. 4, 7. A forms from Eniwetok drill hole E-1, 1925–55 ft. U.S.N.M. colln. (4) transverse section, (7) longitudinal section. Note that the alveolar structure is not visible in the early chambers.

FIGS. 5, 9, 11–13. All from Eniwetok drill hole E-1, 1925–55 ft. (5) P47594, A form; (9) surface view of typical specimen showing fine striae, P47597; (11) longitudinal section through A form; P47599; (12) wall of terminal chamber viewed from inside, × 56, P47600; (13) A form, terminal chamber broken off—note ' step ', P47601.

FIGS. 6, 10. A forms from Eniwetok drill hole E-1, 1996½–2007 ft., P47595 & 47598.

All ex. U.S.G.S. collection.

FIG. 8. A form (P47596) from Bikini drill hole 2B, 2049–2059½ ft. Topotype. Ex U.S.G.S. colln.



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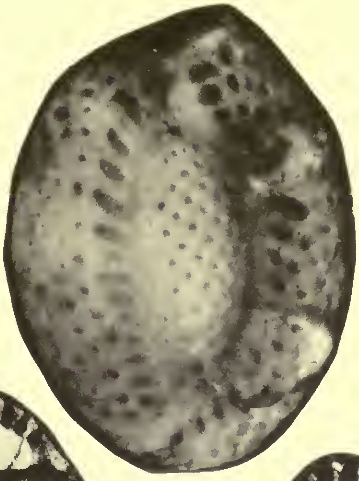

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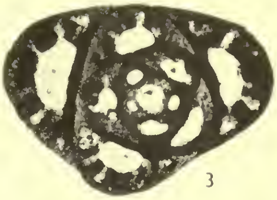

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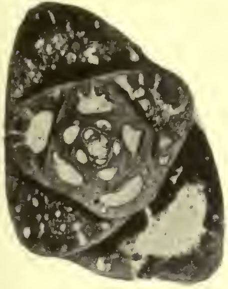

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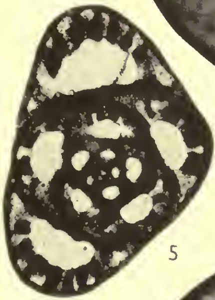

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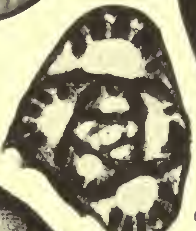

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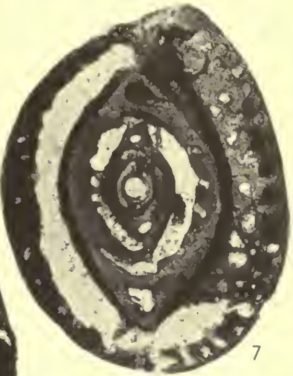

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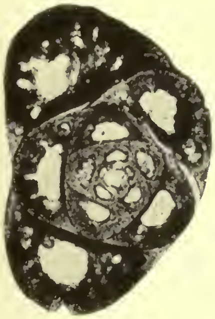

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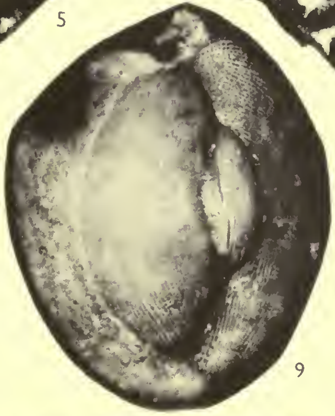

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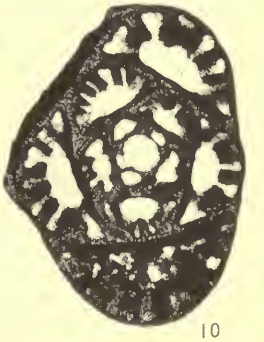

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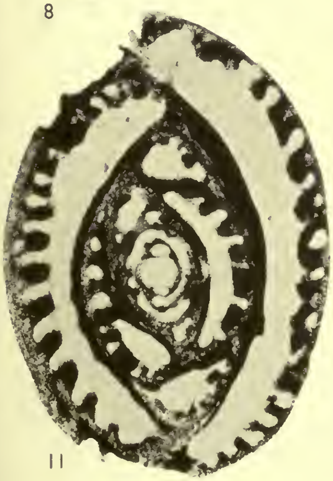

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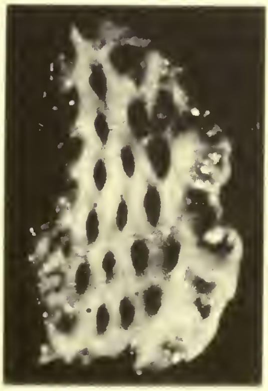

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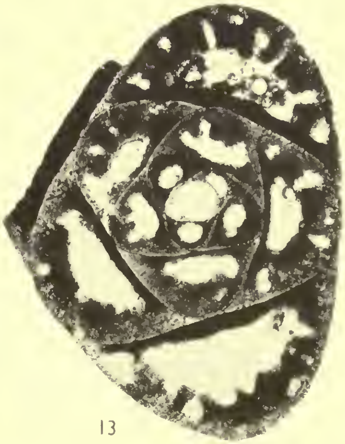

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PLATE 5

The figures on this plate illustrate the difficulty in determining specimens from certain Indo-Pacific (Upper Te) limestones where transitional forms between *A. striata* and *A. howchini* occur, or where the range of variation of *A. striata* overlaps that of *A. asmariensis.*

FIG. 1. ***Austrotrillina*** sp. ×50, P46525. Intermediate between *A. striata* and *A. howchini.* Upper Te, Melinau limestone, Sarawak.

FIG. 2. ***A. striata*** ×52, P46526. Upper Te, Melinau limestone, Sarawak.

FIG. 3. ***A. striata*** ×50, P46522. Lower Te, Melinau limestone, Sarawak.

FIG. 4. ***A.*** cf. ***howchini*** ×50, P46524. Upper Te, Melinau limestone, Sarawak.

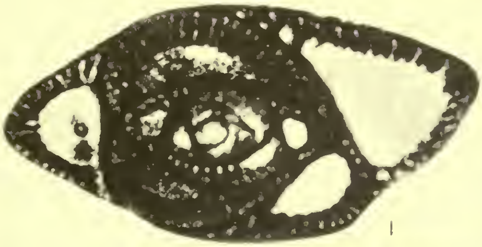
FIGS. 5, 11. ***A.*** cf. ***howchini*** ×50, P47602, P47606. Primitive forms from the Tagpochau limestone, Saipan. Sample No. MSB 413. U.S.G.S. colln.

FIGS. 6, 7. ***Austrotrillina*** sp. ×50. Tagpochau limestone, Saipan U.S.G.S. colln. Sample No. MSB 397, Lower Te. These specimens are not strictly determinable In some respects they resemble *A. asmariensis,* in others *A. striata/howchini* (6) P47603; (7) P47604.

FIG. 8. ***Austrotrillina*** sp. ×50. Tagpochau limestone, Saipan, Sample No. MSB 403, U.S.G.S. colln. Intermediate between *A. striata* and *A. howchini.*

FIG. 9. ***A.*** cf. ***striata*** Todd & Post, B form, ×50, P47605. Tagpochau limestone, Saipan. Ex Sample No. B397, U.S.G.S. colln.

FIG. 10. ***A.*** cf. ***howchini*** ×50. Part of wall of a specimen from the Tagpochau limestone, Saipan. Sample No. MSB 388, U.S.G.S. colln.



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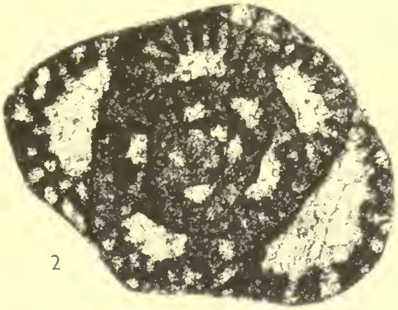

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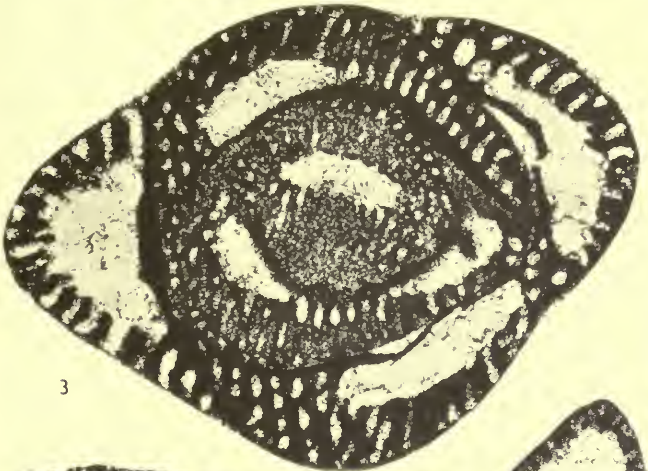

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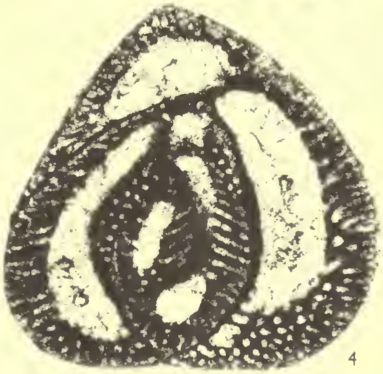

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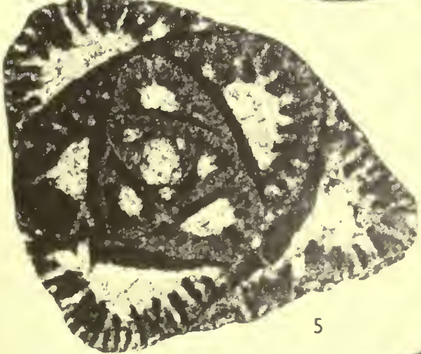

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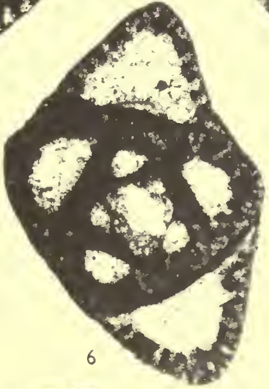

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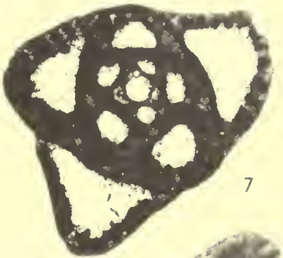

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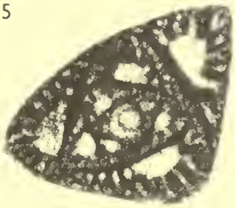

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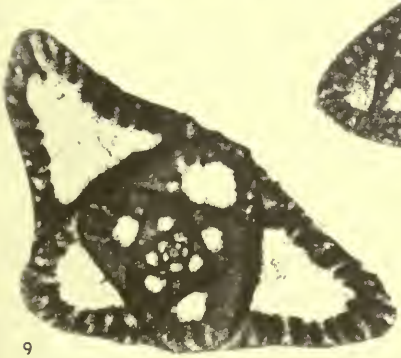

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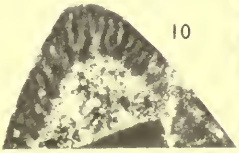

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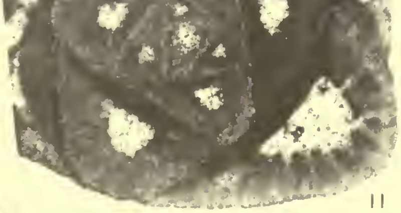

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PLATE 6

FIG. 1. ***Austrotrillina howchini***, A form ×50. Lower Chake beds, south end of Funzi Island, Pemba Island, Tanzania. P22848.

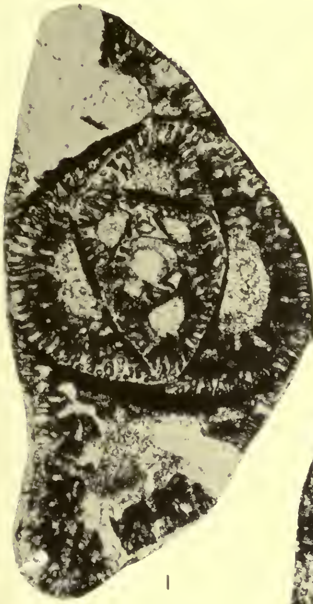
FIGS. 2, 4, 5. ***A. howchini.*** All ×50. P47607 (ex. P29878). All from the Lower Miocene of the Malabar coast, Cochin, Travancore, India. Associated with *Taberina malabarica* (Carter) for which this is the type locality: Carter collection.

FIG. 3. ***A. howchini.*** B form, ×40, P47608. Pata limestone, Chowilla Dam site, South Australia. Lower Miocene (Lower Tf).

FIGS. 6, 8. ***A. brunni.*** Re-illustration of two of Marie's types: ×35 and ×50 approx.

FIG. 7. ***A. howchini.*** Stereoscan electron microscope photograph showing surface pits. The subsurface reticulation is no longer visible as the specimen is coated with a fine gold film. Same individual as Pl. 2, figs. 1, 2. ×750, KV 20.

FIG. 9. ***A. striata.*** Stereoscan electron microscope photograph showing surface striae and pits. Bikini Well 2b, 2091–2102 feet. P47609 ×750, KV20. Note that the pits are smaller than in *A. howchini.*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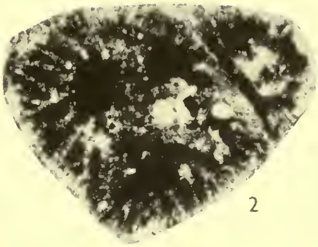
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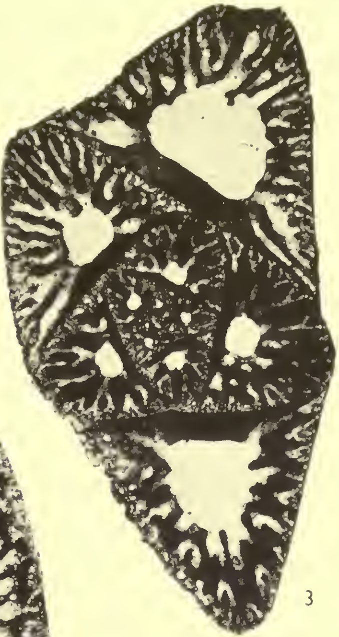
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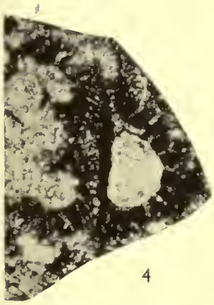
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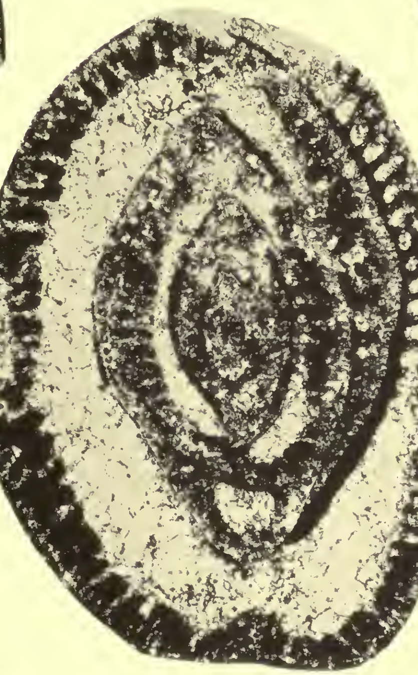
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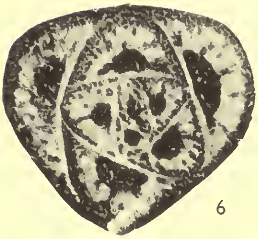
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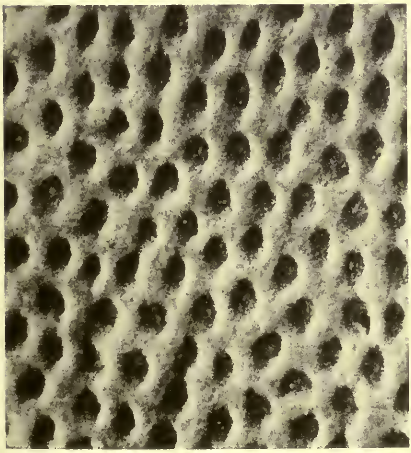
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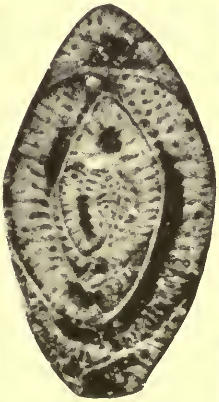
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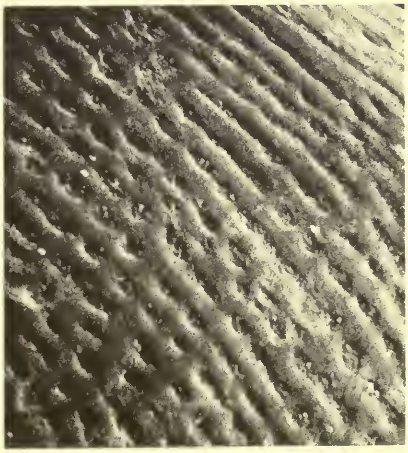
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BRITISH NEOCOMIAN RHYNCHONELLOID BRACHIOPODS

E. F. OWEN
and
R. G. THURRELL

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 3
LONDON: 1968

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BRITISH NEOCOMIAN RHYNCHONELLOID BRACHIOPODS

BY

ELLIS FREDERIC OWEN
British Museum (Natural History)

and

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Pp. 99–123; 4 *Plates*, 8 *Text-figures*

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BRITISH NEOCOMIAN RHYNCHONELLOID BRACHIOPODS

By E. F. OWEN & R. G. THURRELL

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SYNOPSIS

A short stratigraphical account is given of the Lower Cretaceous, Neocomian beds of the southern part of the Lincolnshire Wolds. The Rhynchonellidae collected from these strata and beds of similar age in the northern Wolds, and from the Speeton Clay of Yorkshire are systematically described and compared with the corresponding fauna of the Brunswick and Hanover districts of north-west Germany, and also with faunas described from Neocomian horizons in Switzerland.

INTRODUCTION

It was agreed at the Colloquium on the Lower Cretaceous held at Lyon, France in 1963 (p. 832) that the term Neocomian should not be used as a stage name, but that it should, perhaps, be preserved for a group of stages. It was further agreed that the term should be limited to represent three stages in the Lower Cretaceous namely, Berriasian, Valanginian and Hauterivian, and that the Barremian should be regarded as a separate stage midway between the top of the Hauterivian and the base of the Aptian.

It is difficult when dealing with older classifications and groupings of beds to be precise about the geological age. For this reason, and because the term Lower Cretaceous has a somewhat broader connotation, the term Neocomian as used in this paper sometimes includes reference to the Fulletby beds, generally regarded as of Lower Barremian age.

The material on which this paper is based was collected during the course of field surveys of the Lower Cretaceous rocks of the Lincolnshire Wolds, and from the cliff section at Speeton, Yorkshire. The descriptions of the formations in the southern Wolds are taken from a thesis submitted and approved in 1957 for the degree of Ph.D. of London University by one of the authors (R.G.T.). Many of the species of Rhynchonellidae described here from the Speeton Clay and from the Claxby Beds of Nettleton, Lincolnshire, were collected by Dr. P. Rawson during his study of the northern Wolds for a thesis submitted and approved for the Ph.D. degree of Hull University in 1967.

Brachiopods appear sporadically throughout the British Neocomian but occur most frequently in the C_6–D_2 Beds of Swinnerton at Speeton and in the condensed sequence of the Spilsby and Claxby series southeast of Nettleton. All the forms described here are from three main sources: Beds C_6, D_{1-2} of Speeton Cliff, Yorkshire; Claxby Beds at Nettleton, Lincolnshire [110980]; and the Roach Stone of the Fulletby Beds at Cawkwell [280880], Belchford [290750] and Dalby Park [410700], Lincolnshire. All National Grid references quoted fall within the 100 km. square TF.

Although the area occupied by the outcrop of the lower Cretaceous rocks in Lincolnshire far exceeds that of the Speeton Clay in Yorkshire, they have attracted much less attention. They are generally poorly exposed and even when brick-clay, iron-ore and building stone were being dug during the last century, useful occurrences were few and far between. Efforts to correlate the strata below the Red Chalk were at first attempted on rather tenuous geological evidence. Judd (1870) was the first to employ palaeontological methods, using the ammonites to compare the English facies with rocks at localities he had visited in Europe. A zonal standard of reference had not been established in any region at that time, but later research, mainly at Speeton, resulted in the publication of a zonal scheme based on the belemnites (Lamplugh 1889, 1924), which has remained in use until the present with only minor modifications (see Swinnerton 1936–55).

Lamplugh (1896 : 191–293) showed that the Speeton subdivisions were also recognizable in the Lincolnshire Neocomian, but other workers have preferred the more precise correlations afforded by the ammonite assemblages. Spath (1924) published a comprehensive system of zones for the Lower Cretaceous. Swinnerton (1935) recorded the presence of two additional ammonite faunas in the bottom three feet of the Spilsby Sandstone at Fordington Pumping Station [416714] Lincolnshire and added considerably to knowledge of the stratigraphy and faunas of the Neocomian of the southern Wolds. He proposed (1935, 1936) the lithological subdivisions adopted here, which embody the nomenclature originally proposed in the Geological Survey's memoir (Jukes-Browne 1887) but with further subdivisions inserted and the system of grouping the formations under geological headings extended. In the absence of borehole data, the thicknesses quoted in the following table have been assessed from field mapping, supported by aneroid traverses with allowances made for the effects of superficial movements, structural complications and facies changes.

The most complete and lithologically variable development of the Lower Cretaceous rocks crops out in the southern Lincolnshire Wolds between Fulletby and Spilsby. The general north-westward attenuation of the strata may be attributed to continued uplift of the Market Weighton Axis during Neocomian times with the consequent development of additional non-sequences and changes of facies towards

TABLE I

			Estimated thickness in feet		
			North Willingham	Belchford	Dalby
Langton Series :	Carstone Beds	Carstone Grit	30	33	34
		Carstone Sands and Clay			
		Sutterby Marl			
Tealby Series :	Fulletby Beds	Upper Roach		40	60
		Roach Stone			
		Lower Roach			
	Tealby Beds	Upper Tealby Clay	27	70+	49
		Tealby Limestone	20		
		Lower Tealby Clay	60		
	Claxby Beds	Upper Claxby Ironstone	15	15	29
		Hundleby Clay			
		Lower Claxby Ironstone			
Spilsby Series :	Spilsby Beds	Ferruginous Grit	35	70	60
		Glauconitic Sands			
		Basement Beds			

that area. A number of interpretations of the detailed interrelations and variations of the formations in Lincolnshire have been published (e.g. Wilson 1948 : 54, Swinnerton & Kent 1949 : 73). From the present six-inch survey, the base of the Carstone Grit appears to overstep northwards all formations successively from the Sutterby Marl down to the base of the Upper Tealby Clay, as shown in Fig. 1. Thinning and change of facies within the Fulletby Beds in the same direction results in the disappearance of the Roach Stone north of Scamblesby [275788]. For the same reasons, the Hundleby Clay facies diminishes north-westwards and cannot be traced farther north than Belchford.

The typical lithologies of the strata from which many of the Rhynchonellidae described in this paper have been obtained are outlined below.

Claxby Beds

These beds, named from their well-known occurrence in the old ironstone workings [112963] near Claxby-by-Caister, were first described by Judd (1867 : 245; 1870 : 329) although Dikes & Lee (1837) had previously noticed a " ferruginous band " . . . at the . . . " top of the Green Sandstone " [= Spilsby Sandstone] at Nettleton.

Ferruginous and non-ferruginous lithofacies are distinguishable in Lincolnshire. The former is present in the northern and central Wolds as the Claxby Ironstone; south-east of Belchford [290750] both facies have been mapped, the non-ferruginous Hundleby Clay being recognizable as pale, purplish-grey, silty clay which splits the ironstone at about the middle and appears progressively to replace the lower part, until in the extreme south-east of the Wolds it comes to rest directly upon the Ferruginous Grit of the Spilsby Beds.

From a thickness of fourteen feet at Nettleton, there is no appreciable south-easterly thickening of the Claxby Beds at outcrop for twenty miles. At Harrington [365720] twenty-three feet are estimated to be present and almost thirty feet at

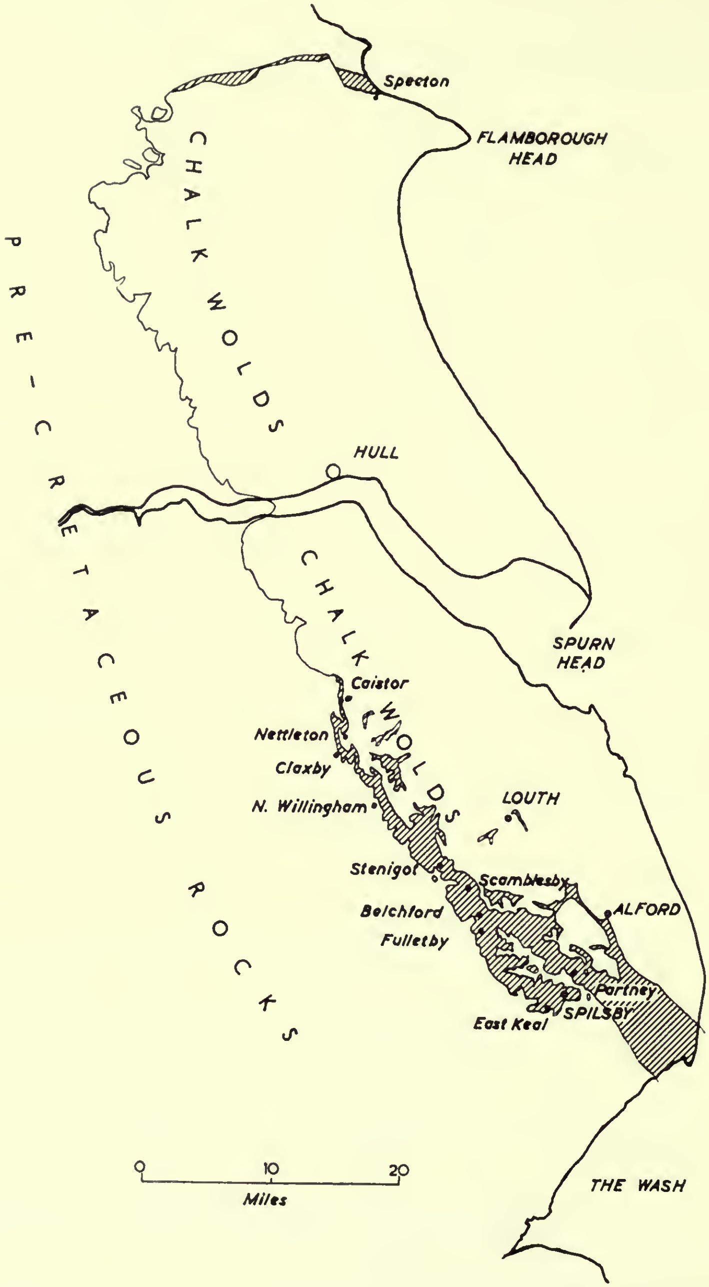

Specton
FLAMBOROUGH HEAD
CHALK WOLDS
PRE-CRETACEOUS ROCKS
HULL
CHALK WOLDS
SPURN HEAD
Caistor
Nettleton
Claxby
N. Willingham
LOUTH
Stenigot
Scamblesby
ALFORD
Belchford
Fulletby
Partney
SPILSBY
East Keal
0
10
20
Miles
THE WASH

FIG. 1. Outcrop and sub-drift occurrences of the Lower Cretaceous rocks in east Lincolnshire and east Yorkshire.

Partney [410680]. The Hundleby Clay is estimated to be up to five feet thick at Belchford, fifteen feet at Hundleby [385640] and eighteen feet at East Keal [375645].

The ironstone facies is characterized by the ubiquitous presence, in varying concentrations, of oolitic iron ore embedded in pale-grey to dark-brown, ferruginous silty clays with pink or cream, calcareous, siltstone bands at some levels. These harder bands contain much less oolitic material than the clays, but both rocks may be hardened and secondarily enriched by ferruginous impregnation and by the oxidation of iron salts to limonitic material which occurs commonly as flaky aggregations in irregular veins and as encrusting " iron pan ".

Glauconite is rare but polished well-rounded pebbles of chert and subangular quartz grit are found, especially about the middle and near the base of the ironstone. Beds of round phosphatic nodules up to four inches across may contain moulds of ammonites, belemnites and " steinkerns " of bivalves. These, together with frequent evidence of contemporaneous erosion, such as the presence of thin beds of broken shells and aggregations of broken and abraded ooliths resting on churned, uneven surfaces suggest that a number of minor non-sequences may exist. Clusters of brachiopods are found more commonly in the oolitic clayey seams than in association with other faunal elements, which appear to have flourished more persistently in the silty environments.

The Hundleby Clay facies normally comprises pale purplish-grey, mottled-brown, silty clay. It tends to become more arenaceous towards the top with yellow-stained shaly micaceous partings. At the type locality, near Spilsby, lenses of coarse, black, pyritous grit and others of white sand up to two inches thick and twelve inches long are present just below the Upper Ironstone, interbedded with irregular bands of decalcified, concretionary, buff-coloured siltstone nodules commonly traversed by irregular fractures infilled by ochreous ferruginous matter. At lower levels the Hundleby Clay characteristically contains less silt and, between Belchford and Hundleby itself, the whole thickness of the formation comprises unctuous, plastic clay wherever it is thick enough to be separately mapped. The sparse macrofauna appears to be devoid of brachiopods.

The Fulletby Beds

Formerly referred to by the Geological Survey as " The Roach " (Jukes-Browne 1887 : 19), the Fulletby Beds were first so called by Swinnerton (1935) from their obvious presence in the cliff-like feature which distinguishes the northern part of Fulletby Hill [300750], the type locality.

The formation is predominantly clayey, essentially ferruginous but rarely glauconitic, so that it is readily distinguishable in the Lower Cretaceous sequence. Exposures, though few, are usually of the Roach Stone. Characteristically reddish-brown clay loams are developed everywhere on these beds.

The Fulletby Beds were subdivided by Swinnerton (1935 : 4) as follows:

	Estimated thickness in feet	
	Fulletby/Belchford	Tetford/Harrington
Upper Roach	10–15	15
Roach Stone	4–6	15
Lower Roach	15–20	30

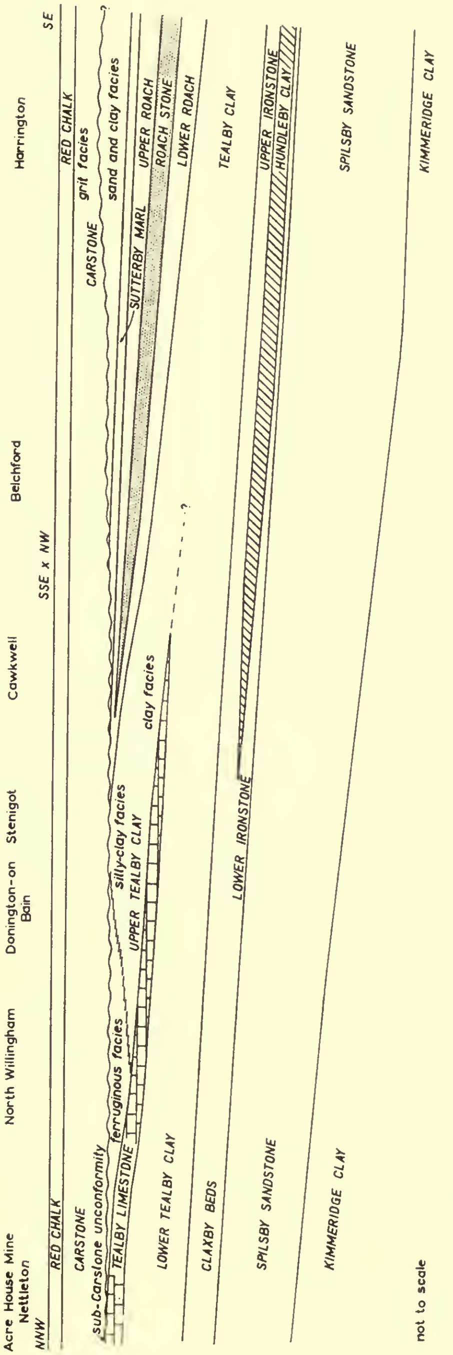
Of all the Lower Cretaceous rocks which crop out in Lincolnshire, these are probably the most variable in thickness and lithology. The clay or silty-clay matrix is commonly dark grey, though it may weather to brown and bright reddish-brown where concentrations of iron ore are particularly high. Grit grains and small rounded (lydite) pebbles are disseminated throughout. Churned horizons, as if brought about by contemporaneous erosion or by organisms, have been observed only rarely.

The Roach Stone crops out just above the middle of the Fulletby Beds, where the predominantly clayey sequence rapidly becomes sandy, somewhat less ferruginous and markedly more calcareous. At a higher level, the arenaceous nature of the Roach Stone is continued into the heavily ferruginous, silty Upper Roach.

The Roach Stone was originally described from the borehole at Alford (Swinnerton 1935 : 10) as a " hard calcreted ferruginous sandstone " approximately twelve feet thick. This description accords well with that given here for the sandstone facies at outcrop. The sandstone, however, is exposed infrequently and it is the ironstone facies which is seen at a number of localities over the whole area, and often it is the sole representative of the Roach Stone, especially in the ground northwest of Fulletby. These facts, especially the last, may suggest that the " ironstone " facies represents a lateral lithological development of the sandstone facies towards the northwest, as well as the indurated equivalent of those Roach beds which lie immediately above and below it in the southern part of the Lincolnshire Wolds. Accordingly, for practical reasons, the Roach Stone is here taken to include all the coherent strata at about the middle of the Fulletby Beds which give rise to mappable lithological and topographical features, irrespective of the previous lithological definition.

The ferruginous content of these beds is predominantly in the form of black or dark-brown polished ooliths or limonite, although there is also a subordinate amount of amorphous and flaky ore, most of which appears to be secondary. The distribution of the indigenous limonite varies greatly; at the outcrop there is very little oolitic material in the Roach Stone or at the extreme base of the Fulletby Beds, but passing upwards in the Lower Roach, the oolitic content gradually increases to a maximum concentration in a bed just below the Roach Stone as defined by Swinnerton (1935) in boreholes. This rock is little more than a compact agglomeration of ooliths with subordinate silty-clay matrix which has sometimes been made coherent at the outcrop by secondary " iron-pan " deposits, but which is more usually friable, and less sandy than Roach Stone. Above the Roach Stone the concentration of oolitic iron ore is high but it appears to decrease, and the fraction of the variegated clay and silty-clay to increase inversely, as the beds are traced upwards towards the base of the Sutterby Marl. At the base of the marl, however, the Upper Roach is again strongly oolitic in some localities (Cawkwell and Sutterby [385720]) but predominantly clayey at others (Dalby Park).

The Roach Stone occurs as two fairly distinct types; an earthy limonite rock and a calcareous sandstone. In the field, both rock types are recognizable in many small exposures, but it is not clear what the inter-relationship of these facies is, either in time or space. Both rock types may be examined in the same general area and both may be much disguised and hardened by secondary " iron-pan " deposits.


NNW
Acre House Mine
Nettleton
North Willingham
Donington-on
Bain
Stenigot
Cawkwell
SSE x NW
Belchford
Harrington
SE
RED CHALK
CARSTONE
Sub-Carstone unconformity
TEALBY LIMESTONE
ferruginous facies
silty-clay facies
UPPER TEALBY CLAY
clay facies
LOWER TEALBY CLAY
CLAXBY BEDS
LOWER IRONSTONE
SPILSBY SANDSTONE
KIMMERIDGE CLAY
not to scale
RED CHALK
grit facies
CARSTONE
sand and clay facies
SUTTERBY MARL
UPPER ROACH
ROACH STONE
LOWER ROACH
TEALBY CLAY
UPPER IRONSTONE
HUNDLEBY CLAY
SPILSBY SANDSTONE
KIMMERIDGE CLAY
?
?

Facies and Thickness Variations at the Lower Cretaceous Outcrop in the Central Wolds of Lincolnshire

FIG. 2.

The sandstone facies is a hard fine-grained, yellowish-brown, evenly bedded siltstone or sandstone cemented by a ferruginous and calcareous ground-mass enclosing scattered grit grains and a few limonite ooliths which are normally evenly distributed but may be more rarely confined to certain layers. The sandstone weathers along moderately strong, rectangular joints into flaggy fragments up to one foot square by about two inches thick, but more massive blocks can be picked up in ploughed fields. Fossils are extremely rare in this facies and no well preserved examples have been collected, but thin sections reveal a limited microfauna.

The ironstone facies is a soft, earthy rock with less sandy material and more oolitic limonite disseminated throughout than in the sandstone facies. It is also much more variable in lithology: primary calcitic cement may be unevenly replaced by tenaceous "iron-pan" and ferruginous veining which makes the collection and development of the sparse shelly fauna a tedious process; secondary calcite crystals may be present in cavities in the rock and encrust exposed blocks. With diminishing arenaceous content the ironstone facies tends to become even more strongly oolitic, softer, and to contain thin bands of broken shell debris, including disarticulated valves of brachiopods. This rock, when weathered, produces reddish-brown heavily ferruginous clayey loam, the true " roach " of the countryman, containing soft, crumbling boulders of ironstone from which a limited fauna of bivalves, belemnites and brachiopods has been recovered. In the Belchford-Fulletby districts, this facies of the Roach Stone also contain fragments of woody debris and peculiar root-like concretions (" fucoids ") made of compact, silty ore.

Hitherto the Fulletby Beds have been regarded as being poorly fossiliferous, and indeed very few fossil genera have been recorded specifically from this subdivision of the Tealby Series. Of a number of brachiopods collected during the field survey, the Rhynchonellidae are now recorded and described for the first time from the English boreal Cretaceous. The brachiopod fauna from the Claxby Ironstone was described in part by Davidson (1874), and a revision of the Rhynchonellidae described by him is given here, with additional descriptions of species from a similar horizon in the Speeton Clay and from the Hanover district of north-west Germany.

SYSTEMATIC DESCRIPTIONS

Superfamily **RHYNCHONELLACEA** Schuchert 1896

Family **RHYNCHONELLIDAE** Gray 1848

Subfamily **CYCLOTHYRIDINAE** Makridin 1955

Genus ***LAMELLAERHYNCHIA*** Burri 1953

Lamellaerhynchia rostriformis (Roemer)

(Pl. 1, figs. 1–6; Pl. 2, figs. 1–9; Pl. 3, fig. 2; Text-figs. 3, 4)

1836 *Terebratula rostriformis* Roemer : 40, pl. 2, fig. 22.
1839 *Terebratula multiformis* Roemer : 19, pl. 18, fig. 8.
1839 *Terebratula rostralina* Roemer : 20, pl. 18, fig. 7.
1841 *Terebratula multiformis* Roemer; Roemer : 37.

1842 *Terebratula rostralina & rostrata* Roemer; Leymerie : pl. 15, fig. 11.
1863 *Rhynchonella multiformis* (Roemer); de Loriol : 113, pl. 15, fig. 23.
1864 " *Rhynchonella depressa* Credner " (in part); Credner : 549, pl. 18, figs. 5–12.
1871 *Terebratula depressa* Quenstedt (*non* Sowerby, 1825); Quenstedt : 155, pl. 41, figs. 2, 6–10.
1872 *Rhynchonella multiformis* (Roemer); Pictet : 10, pl. 195, figs. 5–8.
1913 *Rhynchonella multiformis* (Roemer); Jacob & Fallot : 52, pl. 7, figs. 5–7.
1953 *Lamellaerhynchia multiformis* (Roemer); Burri : 275, fig. 2.
1956 *Lamellaerhynchia rostriformis* (Roemer); Burri : 652, pl. 7, figs. 1, 2, pl. 10, fig. 3.

DESCRIPTION. Biconvex *Lamellaerhynchia* varying from about 18–24 mm. long, 20–26 mm. wide and 12–15 mm. thick with a low median fold on the brachial valve and a correspondingly shallow sulcus in the pedicle valve. In some mature forms there is a marked tendency for the shell to become trilobate where the median fold is poorly developed. The uniplicate anterior margin shows some tendency to asymmetry and marginal thickening. The suberect beak is bordered by well-marked beak-ridges defining a broad, extensive interarea. Outward projections of the conjunct deltidial plates extend posteriorly and encircle a large foramen.

In outline the shell varies from subcircular to elongate-oval to broadly triangular. The umbo varies from short and massive to produced and sharp with incurvature of the beak. In the typical form, the ornament consists of twenty to twenty-four sharply defined, strong, radiating, non-bifurcating ribs on each valve with four to five on the fold and a similar number in the sulcus. In some of the variants the number of costae on each valve depends on the type of rib; some having fine, more rounded costae while others have more numerous but narrower, sharp ribs.

Internal characters. In the original description of the genus *Lamellaerhynchia* Burri (1953 : 276, fig. 3), included a series of thirteen transverse serial sections through the umbo of a specimen under the specific name of *L. multiformis*, from the Hilsconglomerat of Berklingen, Brunswick, north-west Germany, and added a further single section of another specimen from the Lower Hauterivian of Bachbett des Arnon, Switzerland. In a subsequent description of the genus Burri (1956 : 652, 655), correctly quoting the valid name for the type-species of the genus as *Terebratula rostriformis* Roemer, included a further series of transverse sections of a specimen from Bachbett des Arnon, Switzerland.

Comparison of the series of transverse sections made by the authors from topotype material, and those made and published by Burri reveals fundamental differences which are recorded here. Although in general outline the umbonal cavities appear similar, the main differences lie in the distal ends of the hinge-plates which, in the specimen figured by Burri (1953 : 276) from Berklingen, are seen to have a concave dorsal surface and are, in the broadest sense, Y-shaped. The Swiss specimen which Burri (1956 : 655) subsequently figured is shown to have gently curving hinge-plates with no discernible division at the distal ends. The fourteenth section in the series showing the posterior ends of the crura is taken from the same specimen in each case, as admitted by Burri in the legend.

From this discrepancy in the description of the internal structure of *Lamellaerhynchia rostriformis* it must be concluded that Burri does not regard the shape of the hinge-plates as being of diagnostic importance, an assumption confirmed by his description of the genus which bears only a brief reference to that structure. The writers, however, do not share Burri's view and include here a series of transverse serial sections (Text-fig. 3) of a specimen of *L. rostriformis* from Roemer's type locality of Elligser Brink, near Hanover, north-west Germany. It will be seen from this series that the dorsal surfaces of the distal ends of the hinge-plates are concave or broadly Y-shaped (sections 8–10) and are, in fact, similar to those shown in Burri's original series (1953 : 276) from Berklingen. It may also be seen that the extreme posterior ends of the crura do not terminate in the manner of Burri's Swiss specimen i.e. acutely concave or U-shaped with the concave surface directed towards the floor of the dorsal valve. Instead they tend to narrow anteriorly, curving abruptly anteriorly with their concave surface both dorsally and ventrally directed. This stage is regarded as characteristic of *L. rostriformis* and may even be confined to this species since it is not shown in any of the transverse sections of other species of *Lamellaerhynchia*.

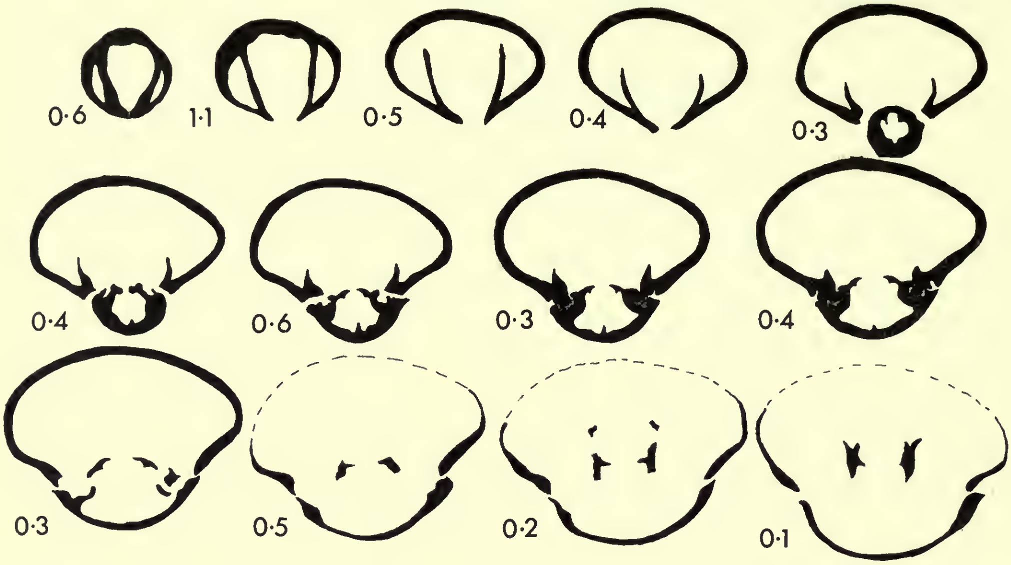


Fig. 3. A series of thirteen transverse serial sections through the umbo of a specimen of *Lamellaerhynchia rostriformis* (Roemer) from the Neocomian of the type locality at Elligser Brink, Hanover, Germany. B.35702. × 2. Numerals denote distance in millimetres between each section.

A specimen from Gros Vahlberg, north-west Germany (Text-fig. 4), preserved in a crystalline limestone matrix, shows this feature and once again demonstrates the concave surface of the ends of the hinge-plates. It should be noted that the dorsal median septum in this specimen appears more strongly developed and this may prove to be a variable character.

Neotype. *Terebratula multiformis* Roemer 1839 is a synonym of the earlier *T. rostriformis* Roemer 1836, which therefore has priority and must be used even though there is no evidence that Roemer ever used the name subsequent to 1836. The type material was housed in the Roemer Collection at the Hildersheim Museum, north-west Germany which was damaged and partly destroyed during the war (1939–45). In order to re-establish the species as *Lamellaerhynchia rostriformis* (Roemer), Burri (1956 : 653), selected a neotype from the remainder of the Roemer collection. This specimen, which he figured (Burri 1956, pl. 7, fig. 1 a–d) is in the Roemer-Museum at Hildersheim, registered number 781a. It is stated to have been collected from the " ' Hilston ' (Astieria-zone = oberstes Valanginien oder Noricuszone = unterstes Hauterivien) " of Elligser Brink, near Hanover.

REMARKS. Roemer's original definition of *Terebratula multiformis* (1839 : 19, pl. 18, fig. 8) was so loosely expressed that it has hitherto been possible to include in it a large number of variable forms which, although they are doubtlessly closely interrelated genetically, may nevertheless be separated generically with advantage. Burri has found it practicable to differentiate between certain of these forms which are morphologically distinct in Switzerland and south-east France. He points out, however, that in north-west Germany the individual species of the genus *Lamellaerhynchia* are less distinct so that the amount of morphological variation produces transitional forms which cannot be assigned with certainty to any of the established species. This observation is reinforced by our experience with the comparatively few specimens collected from Lincolnshire and Yorkshire.

With such a variable species as *L. rostriformis*, and with so little material available from widespread localities, it is impossible to give any statistical data which would be of significance in determining the true morphological characteristics. Specimens collected from limestone localities, although in the main smaller, appear identical in every respect with those collected from the clays. Specimens collected from the Speeton Clay are comparatively rare, so a comparison has been made between limestone forms from Nettleton and those in a softer, more argillaceous, matrix from the " Elligser Brink Schiste " in the Hanover district of Germany. Likewise, specimens collected from limestone localities in Germany, such as Gros Vahlberg have been compared with similar forms from Nettleton in this country. In each case there has been perfect matching of both the typical form and intermediate variants.

From the foregoing description it may appear that such morphological differences in thickness, sharpness and number of costae, overall outline, produced beak and relative size might constitute an argument in favour of taxonomic separation, but no stratigraphical advantage is yet apparent. The variants described as having more numerous rounded costae, more produced beaks and more triangular outline could, perhaps, be referred to a subspecies, but the paucity of well-collected material from the Neocomian in this country and in north-west Germany makes such a separation difficult.

Burri (1956 : 695) does not record the geological range of this species, but it seems almost certain that the earliest record is from the Upper Valanginian and the latest from the top of the Hauterivian.

Jacob & Fallot (1913, pl. 7, figs. 5–7) figured three specimens under the name

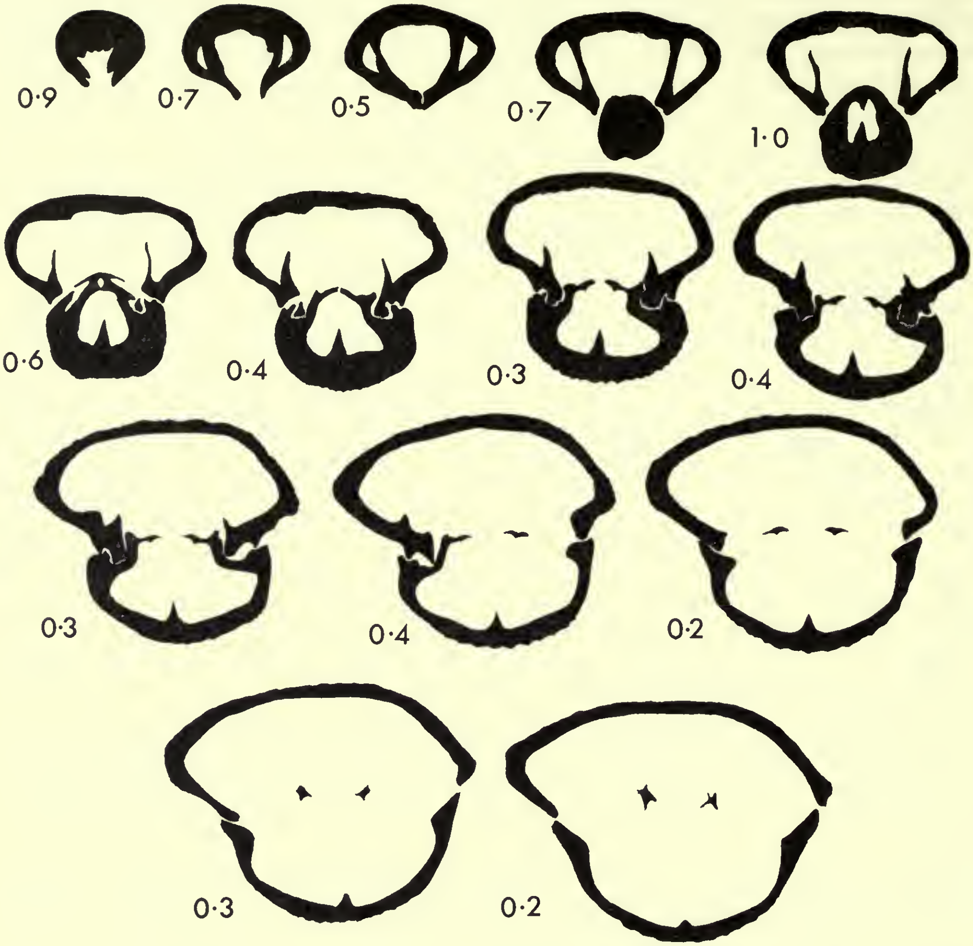


FIG. 4. Another series of fourteen transverse serial sections through the umbo of a specimen of *Lamellaerhynchia rostriformis* (Roemer) from the Neocomian of Gros Vahlberg, north-west Germany. The dorsal septum is shown to be more highly developed and more persistent in this specimen. B.35703. ×2. Numerals denote distance in millimetres between each section.

Rhynchonella multiformis (Roemer). These resemble typical *L. rostriformis*, and illustrate perfectly the breadth of variation in size and type of costation to be found in this species. They were collected from the Upper Valanginian of the Jura Mountains, Switzerland. The specimen represented by fig. 5 is similar in general outline to extreme variants of the species collected at Gros Vahlberg, north-west Germany, and from the Claxby Ironstone at Nettleton and figured here (Pl. 2, figs. 4, 5). They also represent the species *T. rostralina* which Roemer (1840, pl 18, fig. 7) briefly described and figured from the Hils of Schandelahe and Schöppenstedt, near

Hanover. This form is very often found in association with specimens which grade into the typical form and is here considered to be a variant and, therefore, a synonym of *Lamellaerhynchia rostriformis*.

Another notable variant has been found in zone C_7 of the Speeton Clay and departs from the typical form in its type of costation. The costae are less acutely angular and less incised, giving them a more rounded appearance, but in general outline the shell follows the same morphological pattern as the typical form. A specimen illustrating this type of variation is figured on Pl. 2, fig. 9. It is housed in the Hull Museum and registered as 61/64/9. A similar specimen is in the private collection of Mr. R. Clements of Hull University.

In some smaller variants the dorsal fold appears to be more highly developed, with resulting inflation of this valve. These features are often accompanied by a more massive, truncated umbo, slightly smaller foramen and less extensive interarea in the ventral valve.

In spite of its variability *L. rostriformis* can be readily distinguished from other species of *Lamellaerhynchia*, mainly by its larger dimensions, coarser angular costae in the typical form, massive umbo and extensive interarea. As in the case of many described species of *Lamellaerhynchia*, *L. rostriformis* has a tendency to asymmetrical development of the anterior commissure. It also exhibits marked growth-lines on the shell surface, a feature not particularly well developed in other forms of the genus.

DISTRIBUTION. Apart from the English localities of Speeton, Yorkshire and Tealby and Nettleton in Lincolnshire, the species has been collected from the Lower Hauterivian at Auxerre, Yonne, France; Ste. Croix, Switzerland; and Schöppenstedt, Berklingen, Delligsen, Elligser Brink and Gros Vahlberg of the Brunswick and Hanover districts of north-west Germany.

Lamellaerhynchia walkeri (Davidson)

(Pl. 4, figs. 3–8, Text-fig. 5)

1882 *Rhynchonella walkeri* Davidson : 68, pl. 8, fig. 33 only.
1964 " *Rhynchonella* " *walkeri* Davidson; Rudwick : 145, Text-fig. 6A.

EMENDED DIAGNOSIS. Shell subcircular to oval in outline, biconvex. Dorsal valve inflated. Fold and sulcus broad and shallow. Twelve to fourteen coarse, angular ribs on each valve. Umbo short, suberect. Foramen moderate to small, hypothyrid. Deltidial plates conjunct. Beak-ridges distinct, interarea broad, extensive.

LECTOTYPE. Davidson (1882) figured two specimens. Of these, his pl. 8, fig. 33 is a true representative of the species as it is widely known and was collected from the Claxby Ironstone at Acre House Mine, near Claxby, Lincolnshire. The second specimen, figured as pl. 8, fig. 34, departs from this form in ornament and outline and is not a true *L. walkeri*. It is housed in the Museum of the Institute of Geological Sciences (Geological Survey) and is registered as G.S.M. 110258. It is described elsewhere in this paper as *L. walkeri claxbyensis* subsp. n.

The specimen selected as lectotype is, therefore, that figured by Davidson on pl. 8, fig. 33; it is housed in the Sedgwick Museum, Cambridge and registered as S.M.B.11401.

Dimensions of lectotype. Length 18 mm., width 22 mm., thickness 15 mm.

EMENDED DESCRIPTION. In the early growth stages the costation, which is characteristically angular, is already distinct. The curvature of both valves remains costant during development, so that the convexity of the valves is regular right up to the line of the anterior commissure in all but gerontic individuals, in which further growth produces a flattened anterior aspect. The low median fold on the dorsal valve and the shallow sulcus in the ventral valve both develop late and gradually become differentiated from the flanks.

The adult shell is unequally biconvex, approaches an almost spherical outline, and is ornamented by strongly-developed, coarse, angular ribs. There is some variation but the typical form maintains an average length of 16 mm., width of 19 mm. and thickness of approximately 12 mm.

The dorsal valve is strongly convex, becoming increasingly gibbous in the region of the fold which may be occupied by three or four ribs. The broad shallow sulcus in the ventral valve usually develops two or three ribs. A well-marked growth-line is often visible just anterior to the umbonal region, at a point approximately 2–3 mm. from the apex. Otherwise growth-lines are marginal and tend towards lamellar development in older individuals.

Internal characters. These are consistent with those described for the type species with the exception of a somewhat more acute deflection of the hinge-plates towards the floor of the dorsal valve. The broad, concave ends of the radulifer crura are typical.

DISTRIBUTION. *Lamellaerhynchia walkeri* occurs in the Claxby Beds of Lincolnshire, where it is not common. It also occurs in the Neocomian of north-west Germany. Two examples are figured here. Pl. 4, figs. 7, 8 from the Hauterivian of Elligser Brink for comparison with examples from Claxby Ironstone localities.

REMARKS. The degree of variation exhibited by this species is not great and is confined to the coarseness and small number of ribs which are seen throughout all stages of growth, deeply incised on the surface of each valve. The general outline, which is subcircular in the typical form, varies only slightly, becoming more elongate-oval in some and perhaps faintly triangular in other variants. Although no other British Cretaceous species could be easily confused with *L. walkeri* there are other forms which approach this species in general morphology. They differ in their more numerous, less acutely angular ribs, less convex valves and more highly-developed median fold on the dorsal valve.

Lamellaerhynchia walkeri claxbyensis subsp. n.

(Pl. 3, figs. 3, 4)

1882 *Rhynchonella walkeri* Davidson : 68, pl. 8, fig. 34 only.

DIAGNOSIS. Oval to subcircular in outline. Umbo short, suberect. Foramen small. Beak-ridges well marked; interarea broad, short. Median dorsal fold well developed. Costae sharp, undivided. Growth-lines marginal.

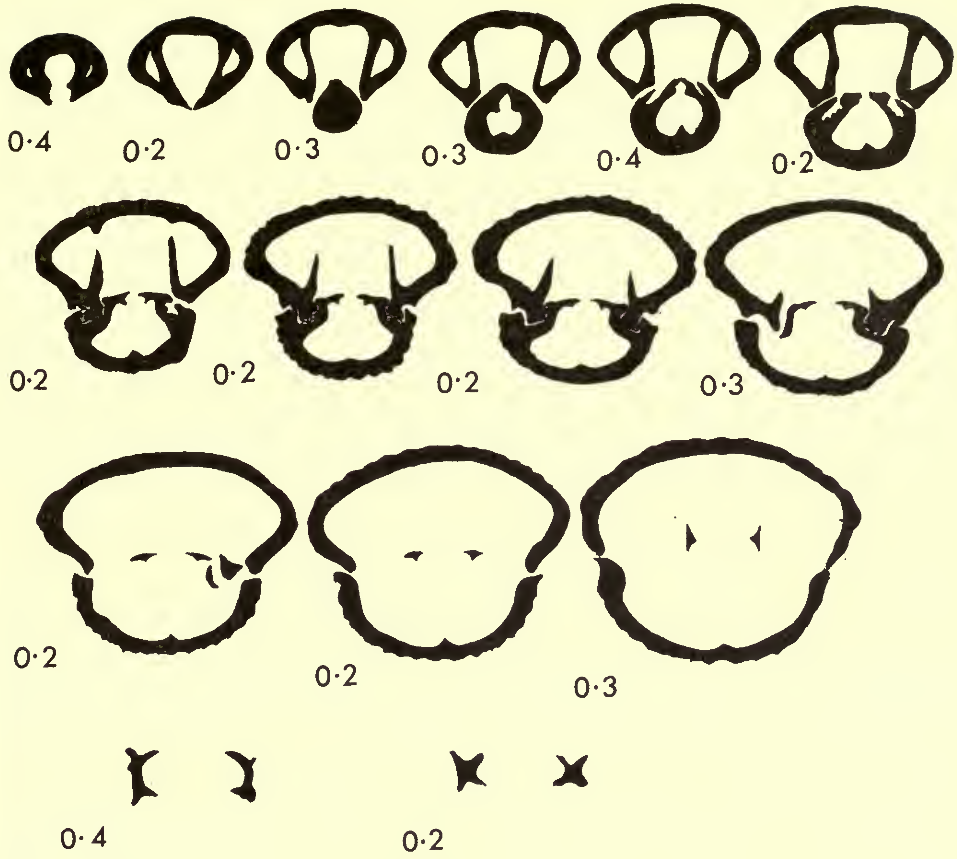


FIG. 5. Fifteen transverse serial sections through the umbo of a specimen of *Lamellaerhynchia walkeri* (Davidson) from the Claxby Ironstone, Nettleton, Lincolnshire. The last two sections show an enlargement (×5) of the distal ends of the crura. BB.44456. ×2. Numerals denote distance in millimetres between each section.

HOLOTYPE. British Museum (Natural History) B.M. BB.42944, from the Claxby Ironstone, Top Mines, Nettleton, Lincolnshire.

Dimensions of holotype. Length 18 mm., width 20 mm., thickness 15 mm.

DESCRIPTION. Although similar in general outline to *L. walkeri* the new subspecies differs from it in having a more highly developed median fold on the dorsal valve, a shorter umbo, and a considerably smaller foramen. The deltidial plates are not well exposed and the broad interarea is shorter or less extensive than in *L. walkeri*. The costae, typically sharp or angular, are considerably more numerous than in *L. walkeri*, and average eighteen to twenty on both valves with four to five on the fold and three to four in the sulcus. Growth-lines are confined to the margins and often become lamellar. This development is well marked on specimens collected from the Claxby Ironstone at Nettleton (British Museum (Natural History), BB.

42945–51). It is also noticeable in specimens from Elligser Brink in north-west Germany, and one specimen illustrating this character is now figured (Pl. 3, figs. 3a–c).

Lamellaerhynchia rawsoni sp. n.

(Pl. 4, figs. 11–15)

DIAGNOSIS. Small *Lamellaerhynchia* about 18 mm. long, 20 mm. wide and 11 mm. thick when fully grown. Distinctly triangular in general outline. Median fold well developed on dorsal valve. Umbo slightly produced, laterally excavated. Deltidial plates conjunct, well exposed. Foramen large, circular. Interarea short, broad, bounded by distinct permesothyrid beak-ridges. Ornament of eighteen to twenty coarse radiating, acutely angular, deeply incised costae. Fold and sulcus with three or four costae.

HOLOTYPE. British Museum (Natural History), B.M. BB.44424, from the Roach Stone of Dalby Park, south Lincolnshire Wolds.

Dimensions of holotype. Length 20 mm., width 21 mm., thickness 14 mm.

PARATYPES. BB.44421,BB.44425, BB.42954 and BB.42955.

DESCRIPTION. Although *L. rawsoni* bears a strong resemblance to *L. hauteriviensis* Burri (1953), from the Lower Hauterivian of Switzerland, it can be readily distinguished by its fewer costae, less well-developed median fold on the dorsal valve, and slightly greater incurvature of the beak. It also has a well-developed growth-line at approximately 2–4 mm. anterior to the dorsal umbo. In older individuals there is a tendency to lamellar thickening of the margins.

Internal characters. As for the type species *L. rostriformis*.

DISTRIBUTION. In the same way that *L. hauteriviensis* Burri is confined to the Lower Hauterivian it would seem that *L. rawsoni* is a species of limited vertical and horizontal range, being found only as a rare fossil in the Lower Barremian, Fulletby Beds, of this country. It has not been identified with certainty from any of the north German deposits though it probably exists in the Barremian of the Hanover area.

Lamellaerhynchia julenia sp. n.

(Pl. 3, figs. 6, 7)

DIAGNOSIS. Elongate-triangular *Lamellaerhynchia* approximately 20 mm. long, 19 mm. wide and 11 mm. thick when fully grown. Produced, suberect beak, laterally excavated. Conjunct deltidial plates well exposed. Foramen large, circular. Acutely angular radiating costae, coarse and deeply incised. Interarea extensive. Beak-ridges distinct, permesothyrid. Anterior commissure with marked tendency to asymmetry.

HOLOTYPE. British Museum (Natural History), B.M. BB.42984, from the Lower Barremian, Fulletby Beds of Dalby Park, south Lincolnshire Wolds.

Dimensions of holotype. Length 21 mm., width 20 mm., thickness 15 mm.

PARATYPE. BB.42985

Description. The outstanding features of this species are its almost equal biconvexity and its constant eighteen to twenty costae on each valve. It is always elongate-triangular in general outline, varying only slightly in width, with a marked tendency to asymmetry of the anterior commissure. It bears a resemblance to *L. gillieroni* (de Loriol) but differs in its coarser, more deeply incised costae and more constantly elongate-triangular outline. It may, nevertheless, be the British equivalent of that species, occurring in the Lower Barremian, as *L. gillieroni* does in Switzerland. The morphological differences described above and the geographical difference would seem to justify the taxonomic separation accorded here.

Internal characters. As for the type species *L. rostriformis* (Roemer).

Distribution. Although *Lamellaerhynchia julenia* occurs only in the Lower Barremian, Fulletby Beds in Britain, a similar form, differing only in relative size occurs in north-west Germany at Schöppenstedt, but the exact horizon has not been recorded. Three good examples of this species from Schöppenstedt are in the British Museum (Natural History), B.M. BB.44460–62.

Lamellaerhynchia cf. ***picteti*** Burri

(Pl. 3, figs. 8, 9)

Description. Acutely biconvex *Lamellaerhynchia* with short, massive umbo, suberect beak and short interarea. The beak-ridges are distinct and permesothyrid. Distinctly subcircular in general outline. Dorsal fold incipient or indistinct with fairly shallow but broad sulcus in the ventral valve. The costae vary in number from between twenty and thirty on each valve but there are some variants with slightly coarser costation and a corresponding reduction in number of costae. Most of the specimens ascribed here to this species show a tendency to asymmetry of anterior commissure.

Remarks. Although this species is compared here to *L. picteti* it is somewhat more circular in outline than the specimens figured by Burri (1956 : pl. 8, fig. 3, pl. 9, fig. 1) but is nevertheless very similar in its type of costation, degree of convexity and general appearance. None of the specimens examined exactly matches those illustrated by Burri and it is for this reason that we have compared our species to the original to give a somewhat broader interpretation.

Distribution. Only three specimens of *L.* cf. *picteti* have been found in Britain so far and these were collected from the Claxby Ironstone at Nettleton, Lincolnshire.

Genus ***RHYNCHONELLA*** Fischer 1809

Rhynchonella parkhillensis sp. n.

(Pl. 4, figs. 9, 10, Text-fig. 6)

Diagnosis. Species of *Rhynchonella* approximately 12 mm. long, 13 mm. wide, and 9 mm. thick when fully grown. Shell biconvex, outline subcynocephalous or tetrahedral. Brachial valve with angular and prominent median fold containing two or three unbranched, simple, deeply-incised costae; sulcus with one or two costae. Beak-ridges distinct, hypothyrid. Umbo suberect. No cardinal process. Shallow septalium. Dental lamellae strong, subparallel. Radulifer crura.

HOLOTYPE. British Museum (Natural History), B.M. BB.42952, from the Fulletby Beds, Roach Stone of Park Hill, Belchford, South Lincolnshire Wolds. Nat. Grid 28907685.

Dimensions of holotype. Length 14 mm., width 14·1 mm., thickness 9 mm.

PARATYPES. BB.52953–55.

DESCRIPTION. In the early growth stages both valves are convex and smooth to within 3–5 mm. from the umbones. At this stage the costae gradually become discernible. A moderately deep sulcus develops and extends posteriorly with a linguiform extension averaging 6 mm. in length. The sulcus tapers gently to form a truncated V-shape. The lateral slopes of the fold are well marked anteriorly, separating the high median portion from the convex flanks, and subsiding completely where the costae arise. The number of costae on the fold varies from two to three. In forms where two costae are developed on the fold, one costa is developed in the sulcus. Likewise, when three costae are developed on the fold, two costae appear in the sulcus.

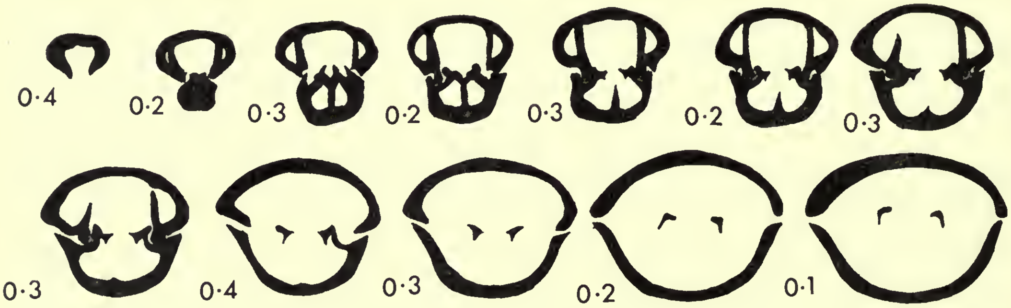


FIG. 6. A series of twelve transverse serial sections through the umbo of a specimen of *Rhynchonella parkhillensis sp. nov.* from the Fulletby Beds, Dalby Park. BB.44405. × 1½ approx. Numerals denote distance in millimetres between each section.

Internal characters. Serial sections made from undamaged examples of this species have been compared with a similar series from *Rhynchonella loxia* Fischer, the type species of the genus, published by Ager (1957 : 8, 9). Dr. Ager has kindly confirmed our assignment of the present species to *Rhynchonella* (s.s.).

REMARKS. *Rhynchonella parkhillensis* is named from its most prolific locality at Park Hill, Belchford, Lincolnshire. The species is rare in the Roach Stone over the ten miles of its outcrop. Preservation is rarely excellent, but the paucity of natural exposures and the ferruginous nature of the matrix increase the value of the few specimens which can be found and extracted undamaged.

Superficially, the species bears a resemblance to other species of *Rhynchonella* (s.s.) as re-defined by Ager (1957), particularly to *R. rouillieri* Eichwald, from the

Russian Upper Jurassic. Ager (1957 : 12) discussed the probable relationship of *R. rouilleri* to other species of *Rhynchonella* and assigned it to this genus. The species was further discussed and several subspecies described and figured by Makridin (1964 : 113, pl. 3, figs. 2–12) from the Upper Jurassic of the Russian Platform. Of these *R. rouilleri eltonica* bears a strong resemblance to *R. parkhillensis*, but the latter can be distinguished by its more acute, triangular outline, slightly more highly developed dorsal fold and more produced umbo. It differs from *R. loxia* in having a less acute, cynocephalous outline and more produced umbo but shares with that species the possession of fine, longitudinal striae, just visible on the surface of the shell in well-preserved specimens. These striae are crossed by transverse growth lines, equally faint in development, which give the appearance of a fine reticulation over the surface of the shell.

DISTRIBUTION. Apart from the type locality at Park Hill, Belchford, specimens have been collected form the same horizon within the Fulletby Beds at Hoe Hill, Fulletby; Cloven Hill, South Ormsby; Dalby Park and Dalby Hill near Spilsby, South Lincolnshire.

Rhynchonella speetonensis Davidson

(Pl. 3, fig. 5, Pl. 4, figs. 1, 2. Text-figs. 7, 8)

1836 *Terebratula varians* Schlotheim; Roemer : 38, II, fig. 12.
1874 *Rhynchonella speetonensis* Davidson : 69, pl. 8, figs. 32a–c.

EMENDED DESCRIPTION. Distinctive, subtrigonal, cynocephalous rhynchonelloid bearing a high fold in the dorsal valve at all stages of growth. Although the species is variable it maintains an average length of approximately 19 mm., width of 20 mm. and thickness of 16 mm. The variations are mainly confined to the width, which may exceed the length by as much as 3–6 mm, and the height of the dorsal fold, which is proportionately greater or more acutely arched in some variants.

No costae are developed but the shell is ornamented by numerous fine, rounded costellae, averaging in number from sixteen to eighteen on the fold and fourteen to sixteen in the sulcus. The costellation varies in size and, in some of the German forms from Ellisger Brink, becomes coarse with a considerable reduction in the number of costellae.

Internal characters. As in the case of *Rhynchonella parkhillensis* transverse serial sections have been made and compared with those of *Rhynchonella loxia*, as figured by Ager (1957 : 8, 9).

LECTOTYPE. Davidson (1874 : 69) described *Rhynchonella speetonensis* from the Speeton Clay of Speeton, Yorkshire and illustrated his description by figuring a specimen (1874, pl. 8, figs. 32a–c) which he said was in the collections of the Woodwardian Museum, Cambridge. In fact, three specimens labelled *Rhynchonella speetonensis*, B.11426, B.11427 & B.11428, from the Speeton Clay are housed in the Sedgwick Museum. Of these, B.11428 is nearest to the somewhat restored drawing of Davidson. It is assumed that all three specimens were used by Davidson and therefore rank as syntypes. B.11428 is selected as lectotype; it is 15 mm. long, 16 mm. wide and 12 mm. thick.

Remarks. The assignment of this species to *Rhynchonella* (s.s.) was made after due consideration of both external and internal morphological features. *R. speetonensis* has many internal structures in common with *R. loxia*, including strong, slightly converging dental lamellae, shallow septalium, short dorsal median septum, similarly-shaped hinge-plates, and radulifer crura. Externally the two species have only two main morphological features in common, namely the general subtrigonal outline and the high cynocephalous median fold in the dorsal valve.

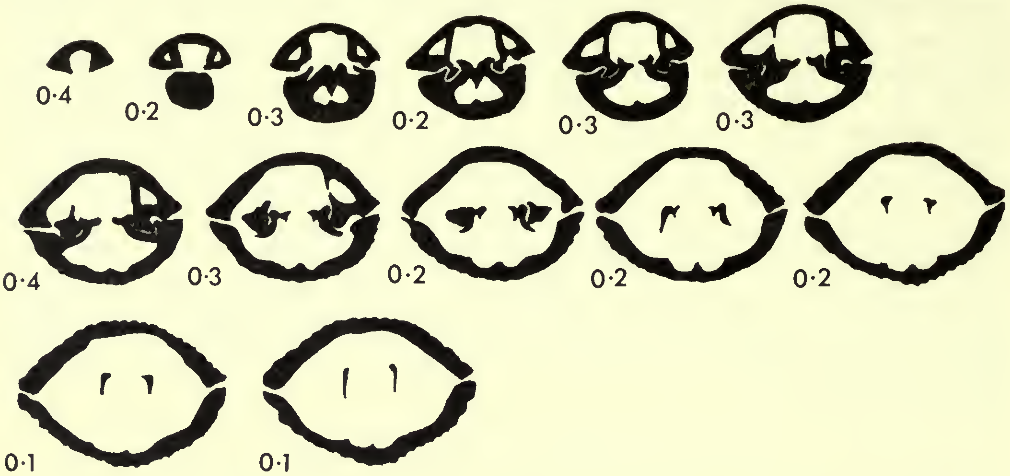


Fig. 7. Thirteen transverse serial sections through the umbo of a specimen of *Rhynchonella speetonensis* Davidson from the Speeton Clay, Speeton, Yorkshire. BB.44458. × 1½ approx. Numerals denote distance in millimetres between each section.

The ornament of fine costellae which distinguishes *R. speetonensis* does not appear on any of the other known species of *Rhynchonella*. However, Ager (1957 : 6) made special reference to faint striae observed on the shell surface of some specimens of *R. loxia*, and noted that Buckman (1918), in discussing the same species, placed sufficient emphasis on this character as to refer to it as capillation. Ager further pointed out that similar fine striae have been seen on specimens of *R. rouillieri* Eichwald from the Lower Volgian of Russia. We have also noted this feature in our description of *R. parkhillensis* sp. n.

In his original description of *R. speetonensis* Davidson (1874 : 69) referred to the numerous growth-lines which cross the main costellation to form a reticulate ornamentation. This is particularly noticeable [see Pl. 3, fig. 5] in specimens from the Speeton Clay but is less well preserved in specimens from the Claxby Ironstone.

The ornament of fine costellae and the high median fold in the dorsal valve, together with a more highly developed or slightly produced umbo, distinguish *R. speetonensis* from all other known species of *Rhynchonella* (s.s.).

Distribution. The species appears to be confined to the Speeton Clay (exact horizon uncertain), the Claxby Ironstone at Nettleton, and the Neocomian Beds at Elligser Brink and in the Hanover district of north-west Germany.

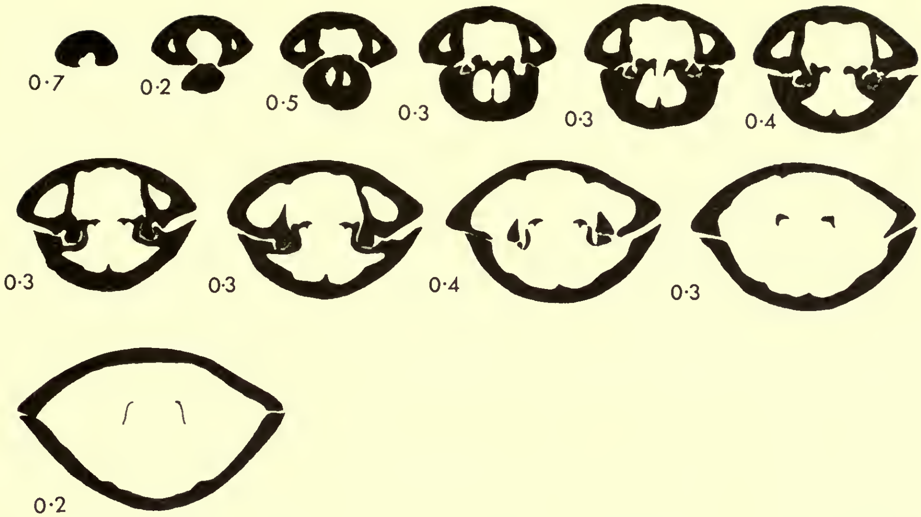


Fig. 8. Eleven transverse serial sections through the umbo of a specimen of *Rhynchonella speetonensis* Davidson from Elligser Brink, north-west Germany. B.11968. ×2. Numerals denote distance in millimetres between each section.

CONCLUSIONS

Since the early descriptions by Roemer (1836; 1840) the north-west German Lower Cretaceous rhynchonelloid fauna has not been further investigated. The paucity of well-collected material from localities of known geological age has made any attempt to correlate the German species with the British forms from Lincolnshire and Yorkshire difficult. A few species have been recognized as occurring on both sides of the North Sea and one of the most important of these is *Lamellaerhynchia rostriformis* (Roemer). This is a variable form, but an attempt is made here to define the broader limits of its variation and to draw a closer comparison between the north-west German specimens and those collected from British localities. In addition, comparison is also made between British and German forms and those described by Burri from the Neocomian of Switzerland.

Although accepting a wide degree of variation within the limits of the species as defined here, it is pointed out that the precise geological range of *L. rostriformis* is unknown and the data obtained are based on specimens collected from Speeton and Nettleton by Dr. R. G. Thurrell and Dr. P. Rawson, and from museum material.

It is thought that any differences in the internal characters between specimens sectioned by the authors (Text-figs. 3, 4) and those previously published by Burri (1953; 1956) are due, in the main, to differences in the technique of making and of presenting drawings of transverse sections.

ACKNOWLEDGMENTS

Our thanks are due to Dr. W. T. Dean and Dr. L. R. M. Cocks of the Department of Palaeontology, British Museum (Natural History), and to Dr. P. Rawson, Queen Mary College, London University. The photographs are the work of Mr. C. B. Keates to whom we also address our thanks.

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PLATE 1

a. Dorsal view. b. Lateral view. c. Anterior view.

FIGS. 1a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Speeton Clay, D 1 Zone, Speeton, Yorkshire. Hull University Coll., H.U.C/S.1590.

FIGS. 2a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. B.M. BB.44406.

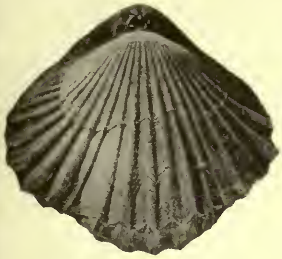
FIGS. 3a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Speeton Clay, Speeton, Yorkshire. Davidson Coll., B.M. 47262.

FIGS. 4a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. B.M. BB.44407.

FIGS. 5a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Speeton Clay, D 2 D Zone, Speeton, Yorkshire. Fletcher Coll., B.M. BB.44459.

FIGS. 6a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Claxby Ironstone, Top Mines, Nettleton, Lincolnshire. Hull University Coll., H.U.C/Rn.302.

All figures at natural size unless otherwise stated. B.M. = British Museum (Natural History).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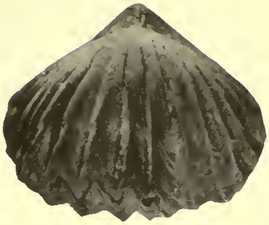
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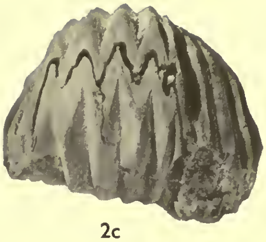
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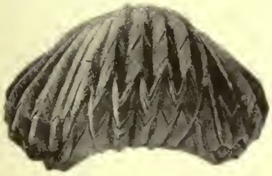
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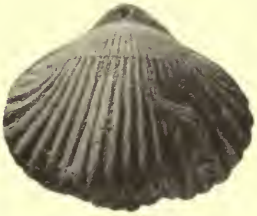
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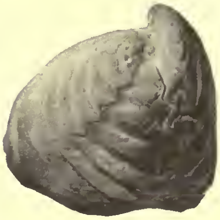
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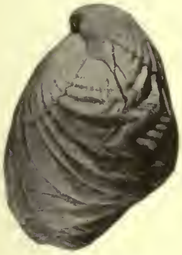
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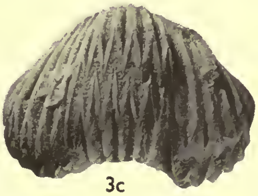
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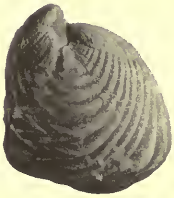
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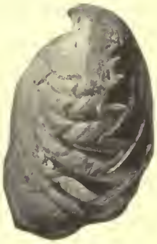
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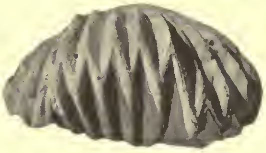
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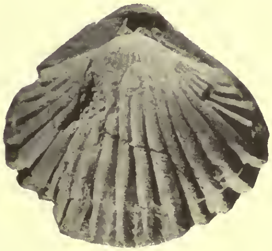
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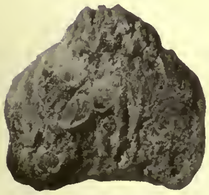
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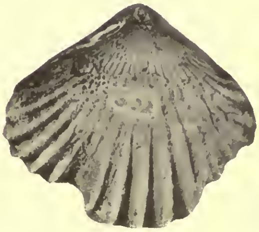
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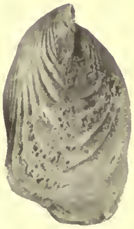
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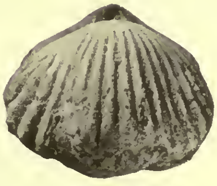
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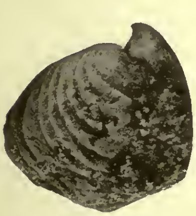
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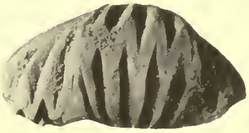
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PLATE 2

a. Dorsal view. b. Lateral view. c. Anterior view.

Figs. 1a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. B.M. BB.44408.

Figs. 2a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Claxby Ironstone, Top Mines, Nettleton, Lincolnshire. Rawson Coll., B.M. BB.44412.

Figs. 3a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Acre House Mine, south of Nettleton, Lincolnshire. C.W. & E.V. Wright Coll., B.M. BB.44413.

Figs. 4a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Acre House Mine, south of Nettleton, Lincolnshire. C. W. & E. V. Wright Coll., B.M. BB.44411.

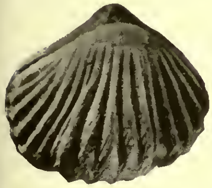
Figs. 5a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Gros Vahlberg, north-west Germany. B.M. BB.44410.

Figs. 6a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Claxby Ironstone, Top Mines, Nettleton, Lincolnshire. Rawson Coll., B.M. BB.44423.

Figs. 7a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. B.M. BB.9094.

Figs. 8a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Speeton Clay, Speeton, Yorkshire. C. W. & E. V. Wright Coll., B.M. BB.44409.

Figs. 9a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Speeton Clay, Speeton, Yorkshire. Hull Museum Coll., 61/64/9.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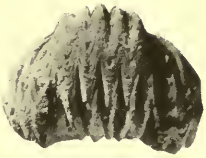
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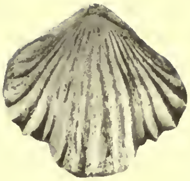
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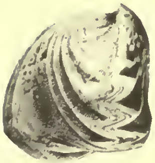
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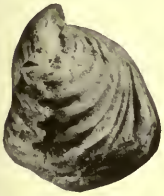
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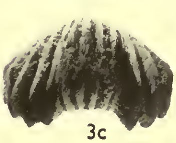
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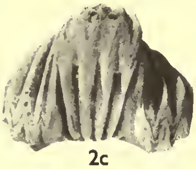
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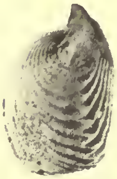
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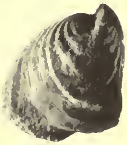
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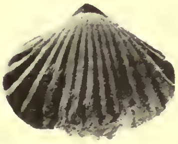
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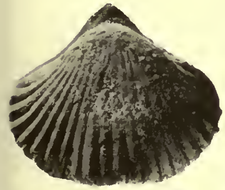
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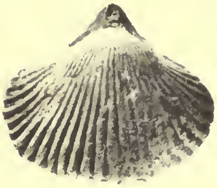
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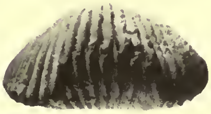
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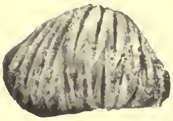
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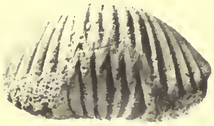
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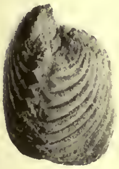
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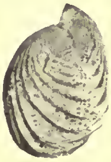
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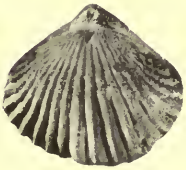
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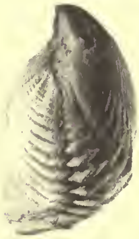
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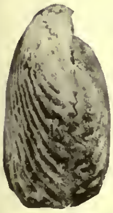
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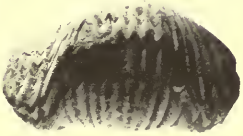
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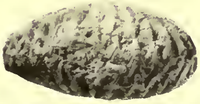
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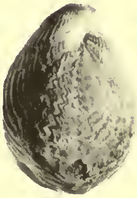
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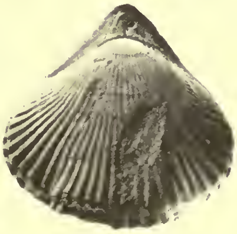
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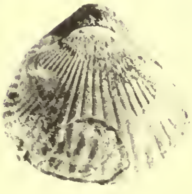
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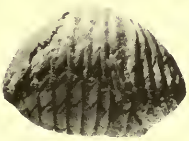
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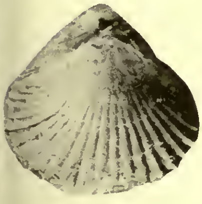
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PLATE 3

a. Dorsal view. b. Lateral view. c. Anterior view.

FIGS. 1a, b, c. ***Lamellaerhynchia*** cf. ***picteti*** Burri. Neocomian, Claxby Ironstone, Top Mines, Nettleton, Lincolnshire. Rawson Coll. B.M. BB.42983.

FIGS. 2a, b, c. ***Lamellaerhynchia rostriformis*** (Roemer). Neocomian, Claxby Ironstone, Acre House Mine, south of Nettleton, Lincolnshire. Institute of Geological Sciences Coll., G.S.M. 110257.

FIGS. 3a, b, c. ***Lamellaerhynchia walkeri claxbyensis*** subsp. n. Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. B.M. BB.44417.

FIGS. 4a, b, c. ***Lamellaerhynchia walkeri claxbyensis*** subsp. n. Neocomian, Claxby Ironstone, Top Mines, Nettleton, Lincolnshire. Rawson Coll., B.M. BB.42944. Holotype.

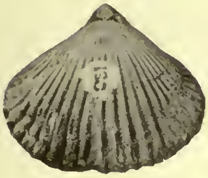
FIG. 5. Enlargement of shell surface of ***Rhynchonella speetonensis*** Davidson to show the transverse lamellar ornament. B.M. BB.44457. ×12 approx.

FIGS. 6a, b, c. ***Lamellaerhynchia julenia*** sp. n. Lower Barremian, Fulletby Beds, Dalby Park, Lincolnshire. Thurrell Coll. B.M. BB.42985. Paratype.

FIGS. 7a, b, c. ***Lamellaerhynchia julenia*** sp. n. Lower Barremian, Fulletby Beds, Dalby Park, Lincolnshire. Thurrell Coll., B.M. BB.42984. Holotype.

FIGS. 8a, b, c. ***Lamellaerhynchia*** cf. ***picteti*** Burri. Neocomian, Gros Vahlberg, north-west Germany. B.M. BB.42987.

FIGS. 9a, b, c. ***Lamellaerhynchia*** cf. ***picteti*** Burri. Neocomian, Schöppenstedt, north-west Germany. B.M. BB.42986.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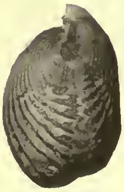
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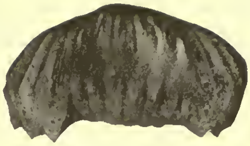
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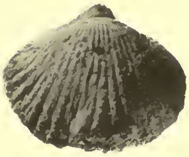
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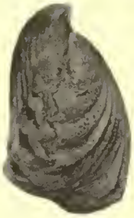
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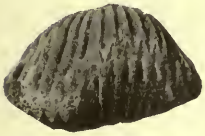
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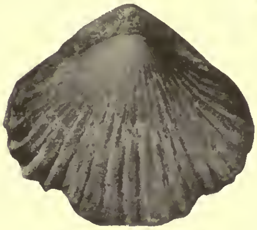
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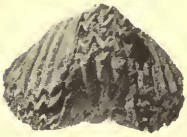
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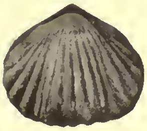
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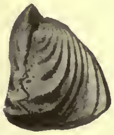
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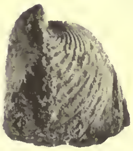
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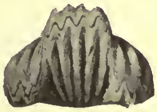
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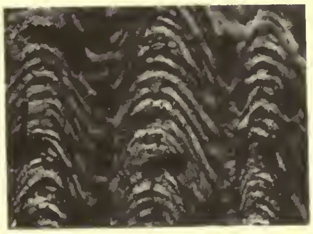
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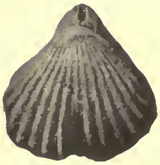
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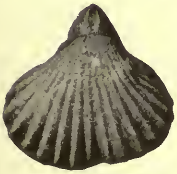
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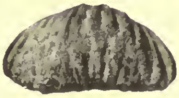
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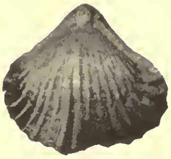
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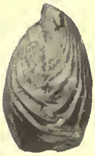
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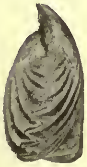
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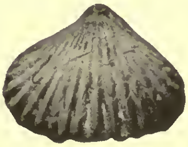
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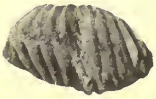
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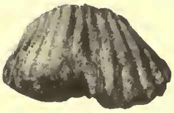
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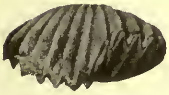
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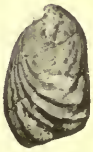
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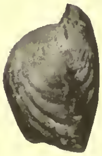
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PLATE 4

a. Dorsal view. b. Lateral view. c. Anterior view.

Figs. 1a, b, c. ***Rhynchonella speetonensis*** Davidson. Neocomian, Claxby Ironstone, Top Mines, Nettleton, Lincolnshire. Hull Univ. Coll. H.U.C./Rn.277.

Figs 2a, b, c. ***Rhynchonella speetonensis*** Davidson. Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. Davidson Coll. B.M. BB.44419.

Figs. 3a, b, c. ***Lamellaerhynchia walkeri*** (Davidson). Neocomian, Claxby Ironstone, Acre House Mine, near Claxby, Lincolnshire. C. W. Wright Coll. B.M. BB.42941.

Figs. 4a, b, c. ***Lamellaerhynchia walkeri*** (Davidson). Neocomian, Claxby Ironstone, Top Mines, Nettleton. Rawson Coll. B.M. BB.42943.

Figs. 5a, b, c. ***Lamellaerhynchia walkeri*** (Davidson). Neocomian, Claxby Ironstone, Acre House Mine, near Claxby, Lincolnshire. C. W. & E. V. Wright Coll. B.M. BB.44414.

Figs. 6a, b, c. ***Lamellaerhynchia walkeri*** (Davidson). Neocomian, Acre House Mine. C. W. & E. V. Wright Coll., B.M. BB.42942.

Figs. 7a, b, c. ***Lamellaerhynchia walkeri*** (Davidson). Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. Davidson Coll. B.M. BB.44415.

Figs. 8a, b, c. ***Lamellaerhynchia walkeri*** (Davidson). Neocomian, " Elligser Brink Schist ", Elligser Brink, north-west Germany. Davidson Coll. B.M. BB.44416.

Figs. 9a, b, c. ***Rhynchonella parkhillensis*** sp. n. Neocomian, Lower Barremian, Fulletby Beds, Roach Stone, Parkhill, Lincolnshire. Thurrell Coll. B.M. BB.42952. Holotype.

Figs. 10a, b, c. ***Rhynchonella parkhillensis*** sp. n. Lower Barremian, Fulletby Beds, Roach Stone, Parkhill. Thurrell Coll. B.M. BB.42953.

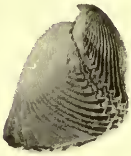
Figs. 11a, b, c. ***Lamellaerhynchia rawsoni*** sp. n. Neocomian, Lower Barremian, Fulletby Beds, Dalby Park, Lincolnshire. Thurrell Coll. B.M. BB.44424. Holotype.

Figs. 12a, b, c. ***Lamellaerhynchia rawsoni*** sp. n. Neocomian, Lower Barremian, Fulletby Beds, Cawkwell, Lincolnshire. Thurrell Coll. B.M. BB.44421.

Figs. 13a, b, c. ***Lamellaerhynchia rawsoni*** sp. n. Lower Barremian, Fulletby Beds, Belchford, Lincolnshire. Thurrell Coll. B.M. BB.44425. Paratype.

Figs. 14a, b, c. ***Lamellaerhynchia rawsoni*** sp. n. Lower Barremian, Fulletby Beds, Dalby Park, Lincolnshire. Thurrell Coll. B.M. BB.42954.

Figs. 15a, b, c. ***Lamellaerhynchia rawsoni*** sp. n. Lower Barremian, Fulletby Beds, Dalby Park, Lincolnshire. Thurrell Coll. B.M. BB.42955.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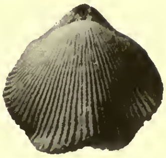
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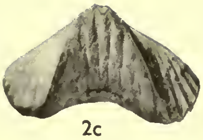
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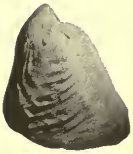
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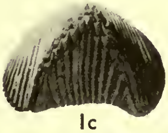
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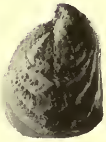
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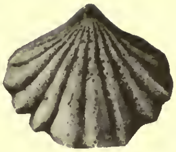
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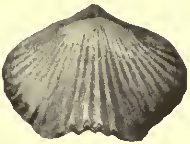
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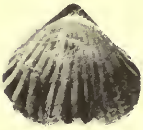
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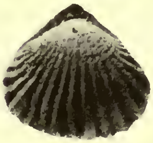
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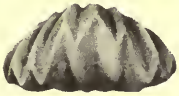
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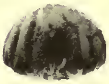
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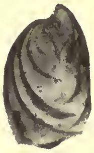
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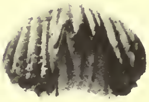
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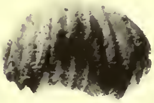
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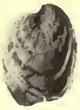
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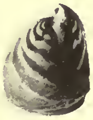
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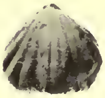
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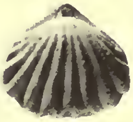
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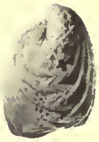
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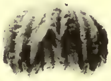
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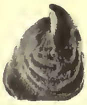
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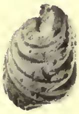
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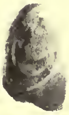
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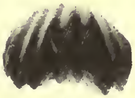
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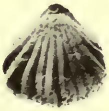
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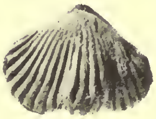
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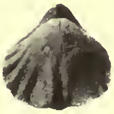
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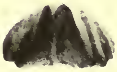
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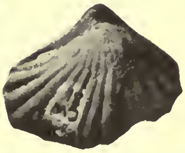
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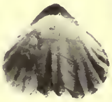
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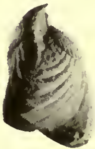
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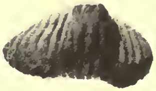
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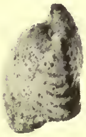
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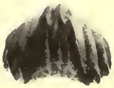
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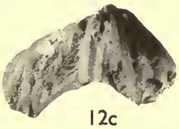
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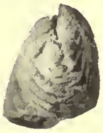
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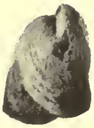
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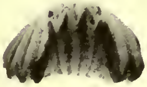
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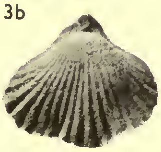
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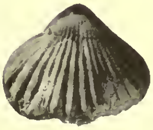
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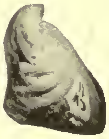
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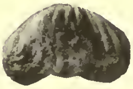
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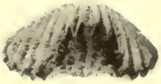
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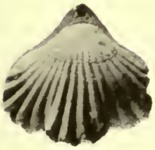
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THE LOWER PALAEOZOIC BRACHIOPOD AND TRILOBITE FAUNAS OF ANGLESEY

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19 APR 1968
NATURAL HISTORY

D. E. B. BATES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 4

LONDON: 1968

THE LOWER PALAEOZOIC BRACHIOPOD AND TRILOBITE FAUNAS OF ANGLESEY

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19 APR 196
NATURAL HIST

BY

DENIS EDWIN BEECHING BATES

University College, Aberystwyth

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THE LOWER PALAEOZOIC BRACHIOPOD AND TRILOBITE FAUNAS OF ANGLESEY

By D. E. B. BATES

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SYNOPSIS

Arenig sandstones, grits and conglomerates rest unconformably on pre-Cambrian rocks and contain a shelly fauna with Baltic affinities, predominantly of brachiopods and trilobites. New brachiopods include *Ahtiella quadrata* sp. nov., *Hesperonomiella carmelensis* sp. nov., *Monorthis typis* gen. et sp. nov., *Panderina lamellosa* sp. nov., *Rectotrophia globularis* gen. et sp. nov., *Reinversella monensis* gen. et sp. nov., *Rhynchorthis rotundus* gen. et sp. nov. and *Pleurorthis costatus* sp. nov. A new trilobite, *Monella perplexa* gen. et sp. nov. is also present.

Higher Arenig and Llanvirn shales, grits, conglomerates, shaley breccias and ironstones contain mixed graptolitic and shelly faunas, including one new brachipood, *Ahtiella concava*.

Lower Caradoc rocks resting unconformably on older Ordovician or pre-Cambrian rocks comprise conglomerates and breccias with shelly faunas, and ironstones and graptolitic shales. A brachiopod-graptolite fauna from Llanbabo and Caregonen can be correlated with the Derfel Limestone fauna of the Arenig district. Limestone blocks in a breccia of the same age yielded a brachiopod-trilobite fauna, including *Protobronteus greenlyi* sp. nov.

Graptolitic shales of Llandovery age at Parys Mountain rest on an acid volcanic group of Caradoc(?) age.

I. INTRODUCTION AND ACKNOWLEDGMENTS

ALTHOUGH Anglesey attracted the attention of several workers in the nineteenth century, our knowledge of the Ordovician stratigraphy is due mainly to the Geological Survey Memoir of Greenly (1919), in which use was made of the standard graptolitic zoning developed by Lapworth, Elles and Wood to date the rocks. The shelly faunas are under-represented in his collections; in particular the important Caradoc fauna from Llanbabo is not represented at all, though a large graptolite fauna is listed from the same locality (Greenly 1919 : 455).

The Ordovician fossils have not been the subject of any intensive study since Greenly's time, or indeed before it. Few species or genera have been erected from among them, and identification has been made in most cases by geologists who were not working on the island. Since the publication of Greenly's memoir two papers have contained accounts of some of the fossils from his collection.

Shirley (1936) in his account of the British Calymenidae referred the calymenids collected by Greenly from the basal beds of the Principal Area to the new species *Synhomalonotus monensis* (now *Neseuretus monensis*), and Whittard (1956 : 17) commented on a specimen of *Ampyx* from the collection. The writer has already described a new species of gastropod, *Matherella*(?) *acuticostata*, from the Arenig Treiorwerth Formation (1963).

I wish to thank Professor A. Williams for his guidance throughout this work, and for his critical reading of the text. The following have commented on specific aspects of the palaeontology: the late Dr. L. R. Cox, Professor C. Poulsen, Professor G. Regnéll, Dr. I. Strachan, Mr. R. P. Tripp, Professor H. B. Whittington and Professor A. Wood.

Much of the work was carried out during the tenure of post-graduate scholarships of the Queen's University of Belfast and the Ministry of Education (Northern Ireland). Further aid was given by grants from the Systematics Association, and the Sir D. Owen Evans fund of the University College of Wales, Aberystwyth.

I am grateful for the help given to me by many friends, including staff and students of the University College of Wales, for their aid in collecting specimens, and for discussions in the field and laboratory.

II. SYNOPSIS OF STRATIGRAPHY

The Ordovician rocks of Anglesey crop out in a number of areas, separated principally by upfaulted blocks of the Mona Complex. In general precise lithological correlations cannot be made between them, although two suites of arenaceous and rudaceous rocks are widespread, one of Arenig age and the other Caradocian.

(a) *Eastern Angelsey*

On the Menai Straits basal conglomerates and grits (the Garth Ferry Grits) rest on the Mona Complex at Garth Ferry, near Beaumaris, and are overlain by shales with *Ptilograptus*. The age of the succession is not known with precision, but since the *Didymograptus extensus* zone is present on the Caernarvonshire shore of the straits between the bridges (Greenly 1919 : 431) the Garth Ferry rocks are probably of approximately the same age.

The area around Llangoed is poorly exposed, but a shelly fauna was collected from grey shales (the Tandinas Shales) at Caregonen. The shales are uncleaved and very soft, grey in colour, with plentiful mica flakes parallel to the bedding. The succession is complicated by north-dipping thrusts, though the shales appear to be dipping at low angles. Greenly found the faunas collected from them per-

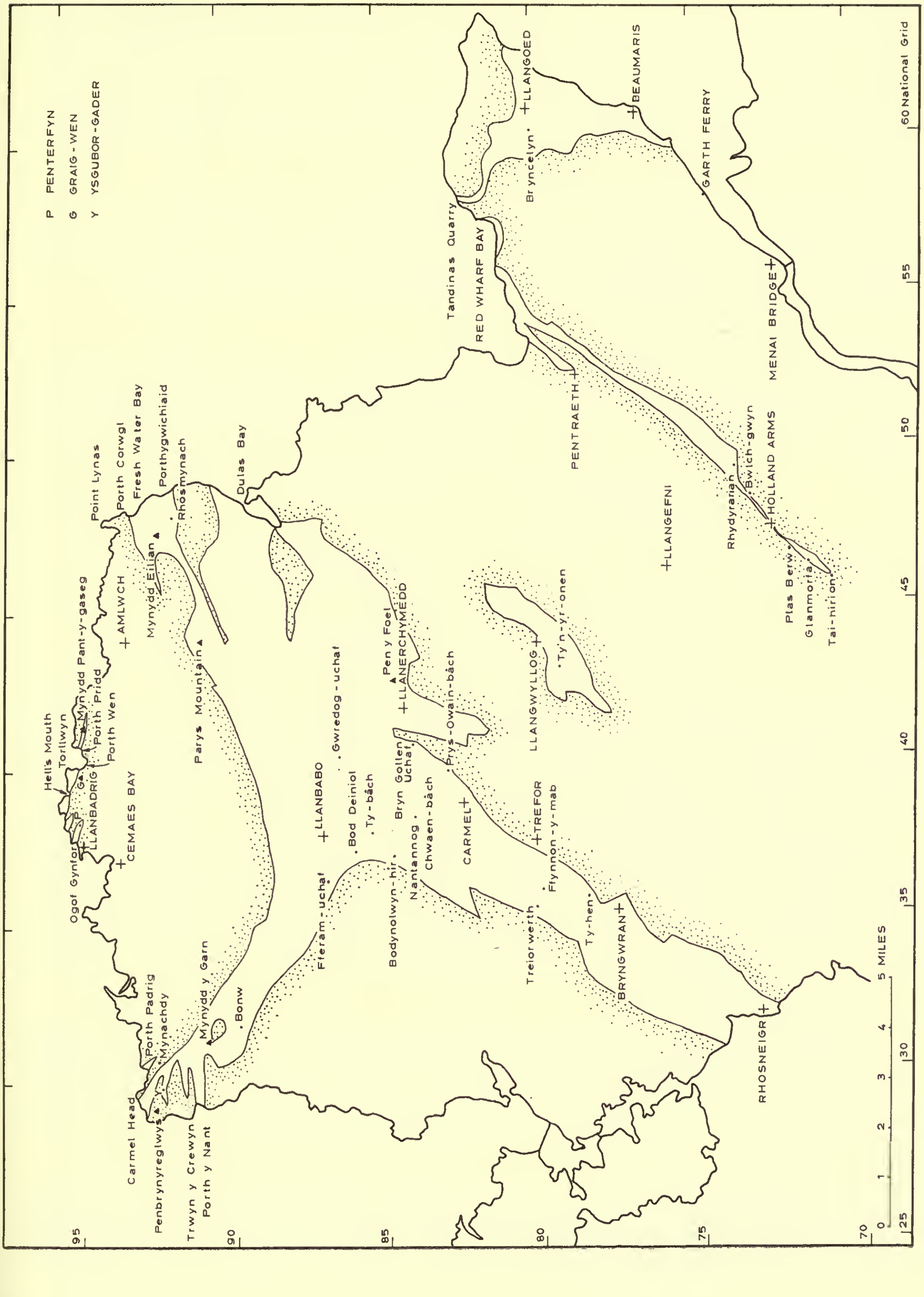
P PENTERFYN
G GRAIG-WEN
Y YSGUBOR-GADER
Hell's Mouth
Torllwyn
Mynydd Pant-y-gaseg
Porth Pridd
Porth Wen
Ogof Gynfor
LLANBADRIG
CEMAES BAY
Point Lynas
Porth Corwgl
Fresh Water Bay
Porthygwichiaid
Rhosmynach
AMLWCH
Mynydd Eilian
Dulas Bay
Parys Mountain
Carmel Head
Penbrynyreglwys
Trwyn y Crewyn
Porth y Nant
Porth Padrig
Mynachdy
Mynydd y Garn
Bonw
Fferam-uchaf
LLANBABO
Gwredog-uchaf
Bod Deiniol
Ty-bâch
Bodynolwyn-hir
Nantannog
Chwaen-bâch
Bryn Gollen Uchaf
Pen y Foel
LLANERCHYMEDD
Prys-Owain-bâch
CARMEL
TREFOR
Ffynnon-y-mab
Treiorwerth
Ty-hen
BRYNGWRAN
RHOSNEIGR
LLANGWYLLOG
Ty'n-yr-onen
LLANGEFNI
PENTRAETH
Tandinas Quarry
RED WHARF BAY
LLANGOED
Bryncelyn
BEAUMARIS
GARTH FERRY
MENAI BRIDGE
Rhydyrarian
Bwlch-gwyn
HOLLAND ARMS
Plas Berw
Glanmorfa
Tai-hirion
95
90
85
80
75
70
25
30
35
40
45
50
55
60 National Grid
0 1 2 3 4 5 MILES

Fig. 1.

plexing (1919 : 433), as they appeared to be of widely different horizons. This was due to Lake's identification of *Ampyx nasutus* Dalman from the shales, a form known to him only from the *Didymograptus bifidus* zone in South Wales, while the graptolites found were typical of the *Nemagraptus gracilis* Zone. The *Ampyx* is however, possibly a new species, while the associated brachiopods are conspecific with those from the Derfel Limestone of the Bala district (Whittington & Williams 1955).

The fauna is: *Climacograptus antiquus* Lapworth (?), *Cl. scharenbergi* Lapworth, *Climacograptus* sp., *Nicolella* sp., *Platystrophia* sp., *Leptestiina derfelensis* (Jones), *Sericoidea abdita* Williams, dalmanellid brachiopod, ogygiid trilobite, *Ampyx* sp. (2), *Sphaerexochus* sp., *Amphilichas* sp. (2), lamellibranch, *Echinosphaerites* sp.

(b) *The Berw Fault Complex*

Ordovician rocks (the Berw Group) incorporated in the Berw Fault complex, crop out at intervals from Pentraeth, at the head of Red Wharf Bay, to Tai Hirion, south-west of Holland Arms, a lower arenaceous division being succeeded by blue shales.

Berw Group	Glanmorfa Shales	Blue shales	?
	Dryll Formation	Greywackes with interbedded shales	300 ft.
	Berw-Uchaf Grits	Quartz grits and sandstones	60–100 ft.

North-east of Holland Arms the basal rocks are poorly exposed, but at Bwlch Gwyn a small exposure of sandstone and shale appears to rest on a pre-Ordovician felsite (Greenly 1919 : 435), though the junction is probably faulted. The sandstone has yielded: *Lenorthis proava* (Salter), *Skenidioides* sp., *Rhynchorthis rotundus* gen. et sp. nov., *Estlandia* (?) sp.

The same horizon is exposed in Rhyd-yr-arian ravine, where the stream is crossed by the road; the following list is from the collections of Greenly and the writer: *Didymograptus hirundo* Salter, *Lenorthis proava* (Salter), *Pleurorthis*(?) sp., *Rhynchorthis rotundus* gen. et sp. nov., *Monorthis*(?) sp., *Reinversella monensis* gen. et sp. nov., *Rectotrophia*(?) sp., *Antigonambonites*(?) sp., polyzoan, crinoid ossicles.

(c) *The Llangwyllog Area*

The faulted outlier around Llangwyllog is also poorly exposed; though no shelly fossils have been found the succession commences with an arenaceous division which is at youngest Llanvirn (Greenly 1919 : 437). Higher shales are Caradoc in age, and an ironstone is present (the Ty'n-yr-onen Ironstone).

(d) *The Principal Area*

In the Principal Area the succession is more complete than elsewhere. The basal arenaceous beds of conglomerate, grit and current-bedded sandstone (the

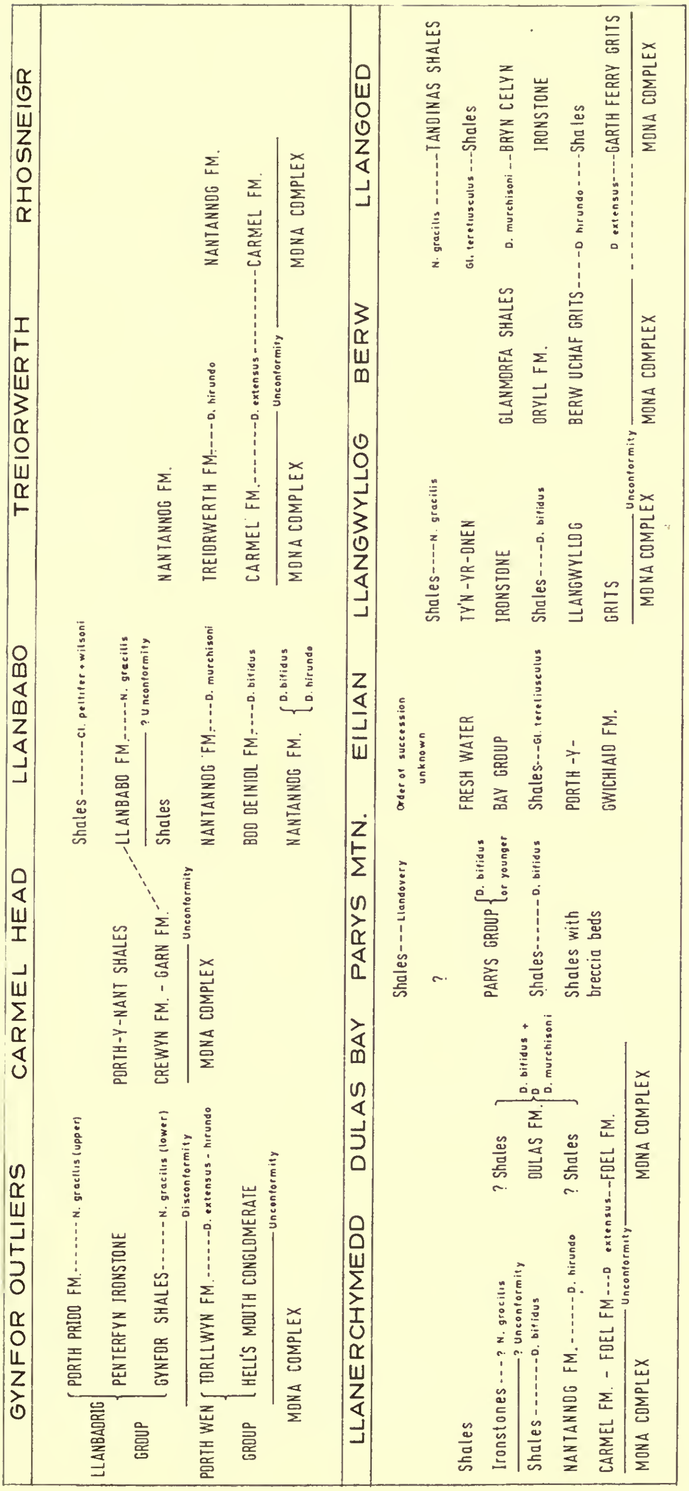
GYNFOR OUTLIERS
LLANBADRIG GROUP
PORTH PRIDD FM.------N. gracilis (upper)
PENTERFYN IRONSTONE
GYNFOR SHALES------N. gracilis (lower)
Disconformity
PORTH WEN GROUP
TORLLWYN FM.------D. extensus - hirundo
HELL'S MOUTH CONGLOMERATE
Unconformity
MONA COMPLEX
CARMEL HEAD
PORTH-Y-NANT SHALES
CREWYN FM. - GARN FM.
Unconformity
MONA COMPLEX
LLANBABO
Shales-------Cl. peltifer + wilsoni
LLANBABO FM.-----N. gracilis
? Unconformity
Shales
NANTANNOG FM.---D. murchisoni
BOD DEINIOL FM.---D. bifidus
NANTANNOG FM. D. bifidus D. hirundo
TREIORWERTH
NANTANNOG FM.
TREIORWERTH FM.---D. hirundo
CARMEL FM.------D. extensus
Unconformity
MONA COMPLEX
RHOSNEIGR
NANTANNOG FM.
CARMEL FM.
MONA COMPLEX
LLANERCHYMEDD
Shales
Ironstones---? N. gracilis
? Unconformity
Shales------D. bifidus
NANTANNOG FM.------D. hirundo
CARMEL FM. - FOEL FM---D extensus
Unconformity
MONA COMPLEX
DULAS BAY
? Shales
DULAS FM. D. bifidus + D. murchisoni
? Shales
extensus--FOEL FM.
MONA COMPLEX
PARYS MTN.
Shales---Llandovery
?
PARYS GROUP D. bifidus or younger
Shales------D. bifidus
Shales with breccia beds
EILIAN
Order of succession unknown
FRESH WATER
BAY GROUP
Shales--Gl. tereliusculus
PORTH-Y-
GWICHIAID FM.
LLANGWYLLOG
Shales---N. gracilis
TY'N-YR-ONEN
IRONSTONE
Shales---D. bifidus
LLANGWYLLOG
GRITS
Unconformity
MONA COMPLEX
BERW
GLANMORFA SHALES
ORYLL FM.
BERW UCHAF GRITS
MONA COMPLEX
LLANGOED
N. gracilis ------TANDINAS SHALES
Gl. tereliusculus ---Shales
D. murchisoni --BRYN CELYN
IRONSTONE
D hirundo ---Shales
D extensus---GARTH FERRY GRITS
MONA COMPLEX

Fig. 2.

Carmel Formation, the Foel Formation) crop out mainly along the south-east boundary lying unconformably on the Mona Complex. The Carmel Formation is exposed from Rhosneigr to within a mile of Llanerchymedd, and comprises a lower fossiliferous division of sandstones and conglomerates, and an upper sparsely fossiliferous division with current bedding. The chief fossiliferous localities are:

(i) by the roadside one-eighth of a mile north-west of Ty-hen (Greenly 1919 : 442). *Lenorthis proava* (Salter), *Hesperonomiella carmelensis* sp. nov., *Neseuretus monensis* (Shirley), *Ogygiocaris selwynii* (Salter), *Monella perplexa* gen. et sp. nov.
(ii) in the scarp above Prys-owain-bach cottage, Carmel. *L. proava*, *H. carmelensis*, *M. perplexa*.
(iii) small quarry pit 100 yds. north-west of Chaen-bach. *Ogygiocaris* sp., *N. monensis*.

The type material of *Monella perplexa* comes from an old quarry, now filled in, 400 yds. north of Bryn Gollen Uchaf, half a mile west of Llanerchymedd.

The Foel Formation is at least a partial lateral equivalent of the Carmel Formation, and only occurs east of Llanerchymedd. It consists of conglomerates succeeded by flaggy sandstones with shale partings, but has so far proved unfossiliferous.

Above the basal rocks are five variable rudaceous and arenaceous formations ranging in age from the *D. extensus* zone to the *D. bifidus* zone; they pass laterally and vertically into poorly exposed shales which contain faunas from the *D. murchisoni* zone.

The Treiorwerth Formation is a thick series of sandstones, grits and conglomerates derived from Mona Complex schists and jaspers, exposed between Rhosneigr and Treiorwerth, and resting on the Carmel Formation. South-east of Ffynnon-y-mab, Trefor, the lowest horizons consist of grey-green siltstones with coarse micaceous shale partings, which pass up through 350 ft. of siltstones and sandstones to coarse grits and conglomerates which are typical of the formation. Three hundred yards south-east of Ffynnon-y-mab (Greenly 1919 : 442) graptolite fragments in the sandstones were identified by Elles as ?*Tetragraptus headi* (Hall). Sandstones in the same outcrop have a rich fauna, occurring as water-sorted lenticles of disarticulated valves: *Lenorthis proava* (Salter), *Monorthis typis* gen. et sp. nov., *Pleurorthis costatus* sp. nov., *Panderina lamellosa* sp. nov., *Hesperonomiella*(?) sp., *Skenidioides* sp. (1), *Rhynchorthis rotundus* gen. et sp. nov., *Reinversella monensis* gen. et sp. nov., *Rectotrophia globularis* gen. et sp. nov., *Porambonites* (s.s.) sp., *Tritoechia* sp., *Antigonambonites pyramidalis* sp. nov., *Matherella*(?) *acuticostata* Bates, *Monella*(?) sp., polyzoan fragments, crinoid ossicles.

The Nantannog Formation is a thick sequence of shales, with a variable rudaceous content, mainly as scattered pebbles and slabs of phyllite, but sufficiently concentrated at certain horizons to produce grits and conglomerates with a shaley matrix. The lithology persisted from the *D. extensus* to the *D. murchisoni* zones, and some of the lower horizons contain brachiopods of the Nantannog Formation fauna. A fauna indicative of the *D. bifidus* zone was found by Greenly at two localities, on the same strike. From the first, west of the road at the bend 200 yards west of Fferam-uchaf farm, Llanbabo, Greenly's specimens were re-examined, no more having been found: *D. bifidus* (Hall), *D. hirundo* Salter, *Orthambonites* (?) sp. (1).

A shelly fauna was found at the second locality, 190 yards south-east of the farm: *D. bifidus* (Hall)(?), *D. hirundo* Salter(?), *Lingula* sp., *Orthambonites*(?) sp., *Skenidioides* sp. (2), *Ptychopleurella* sp., *Dactylogonia* sp., polyzoan fragments, crinoid ossicles.

Two hundred and fifty yards west-south-west of Fferam uchaf Greenly (1919 : 452) found *D. murchisoni* (Beck), and his collection also contains: orthid brachiopod, illaenid pygidium, *Bergamia*(?) sp., *Placoparia* sp., *Cyclopyge*(?) sp.

Laterally and vertically the Nantannog Formation passes into shales or the Treiorwerth Formation, except at Bod Deiniol, south of Llanbabo, where it is succeeded by a thick succession of conglomerates, pebbly grits and sandstones, the Bod Deiniol Formation. The most prominent member is a conglomerate, 80 ft. thick, which occurs near the base of the formation and forms a scarp south of Bod Deiniol. The formation probably belongs to the *D. bifidus* zone, as Greenly records graptolites from low in the zone at Bodynolwyn-hir (1919 : 444) in beds underlying the grits, and beds about 100 ft. above the conglomerate member exposed in the bed of the River Alaw have yielded a pendent *Didymograptus*. The formation loses its topographic expression to the south-east towards Ty-bach cottage, and the grain size becomes finer, although the conglomerate may here be concealed by drift. Fifty yards north of the cottage the writer succeeded in obtaining a fauna from massive grits—probably from a horizon above the conglomerate—when a trench was being excavated in connection with the building of the Alaw reservoir: *Lenorthis* sp., *Panderina*(?) sp., *Paurorthis*(?) sp., *Apomatella*(?) sp., *Ahtiella concava* sp. nov.

North of Dulas Bay a succession of alternating sandstones and shales, the Dulas Formation, with worm burrowing, cone-in-cone concretions, neptunian dykes and current bedding, is well exposed on the shore and poorly inland. On the shore it is faulted against shales containing *D. bifidus* and *D. murchisoni* zone faunas.

Over much of the Principal Area shales are poorly exposed, and Greenly records both lower Ordovician and Caradoc faunas from a number of localities; no formal stratigraphic name is however proposed for them. One new locality, 100 yards north of Gwredog-uchaf, Rhodogeidio, has a graptolite–trilobite fauna: *Dictyonema* sp., *D. bifidus* (Hall), *D. artus* Elles & Wood, *D. stabilis* Elles & Wood, *Climacograptus* cf. *scharenbergi* Lapworth, *Climacograptus* sp., *Glossograptus hincksii fimbriatus* (Hopkinson), *Bergamia*(?) sp.

At Parys Mountain a volcanic suite (the Parys Group) rests on shales (the Parys Shales) of the *D. bifidus* zone or later: graptolites have been found in tips from shafts sunk beneath the volcanic rocks at the west end of the mountain (Greenly 1919 : 458). Although Greenly described the shales immediately beneath and to the north of the igneous rocks as Hartfell in age there is no palaeontological evidence for this. The igneous suite, described by Greenly as a felsite sill, is a complex of rhyolites, autobreccias, ignimbrites, tuffs and shales, intensively cleaved, sheared and silicified (Hawkins 1966 : 13). Above the Parys Group, in the core of the syncline, is a succession of shales and mudstones of Silurian age whose relation to the older rocks is unknown.

Llandeilo fossils (Greenly 1919 : 465) have been found associated with an ironstone at Bonw, and also in a borehole at Llangoed (Greenly 1919 : 432). The extent and thickness of Llandeilo rocks is, however, unknown.

Caradoc rocks are well exposed in the north-west of the Principal Area, where a variable group of basal rudaceous rocks overlies the Mona Complex. On Mynydd-y-garn and at Porth Padrig, north of Mynachdy, on both sides of the Carmel Head thrust a thick series of breccias, overlain by shales and alternating breccia beds (the Garn Formation), rests on several horizons in the Complex. The breccia contains slabs of schists and phyllites up to several feet long, and also rounded blocks of shelly limestone; at Porth Padrig, Greenly records a graptolite fauna from the *N. gracilis* zone in the shales, and the blocks have yielded: *Cyrtonotella* sp. (2), *Palaeostrophomena*(?) sp., *Ptychoglyptus* sp., *Kiaeromena*(?) sp., *Camerella* sp., *Metacamerella* cf. *balcletchiensis* (Davidson), *Protobronteus greenlyi* sp. nov., *Illaenus* sp., *Stenopareia* sp., *Selenoharpes*(?) sp., *Pliomerops* sp.

On Pen-bryn-yr-eglwys, and on the coast to the south, the Mona Complex is overlain by a sandy and gritty formation, the Crewyn Formation, which varies in thickness between 60–150 ft. About 2 ft. above the unconformity, 300 yds. east of Trwyn y Crewyn poorly-preserved shells were found: *Orthambonites* sp., *Plaesiomys* sp., *Platystrophia*(?) sp., lamellibranch, crinoid ossicles.

West of Mynachdy, around an old barn called Ysgubor-gader, is a complicated region of folded and faulted shales, grits and pre-Cambrian rocks. Two small exposures of grit, apparently resting on the pre-Cambrian, are poorly exposed 225 yds. south-west and 400 yds. west-south-west of the barn, and contain *Plaesiomys* cf. *robusta* (*Bancroft*), *Orthambonites*(?) sp. *Dalmanella* (s.l.) sp. and a cystid plate.

In the Llanbabo region Caradoc rocks either rest on or are faulted against gritty beds of the *D. murchisoni* zone, but the contact is not exposed (Greenly 1919 : 451–456). The most complete section is seen at Fferam-uchaf where the rocks strike east-west through the farmyard:

Llanbabo Formation	Llanbabo Church Grits	Pebbly grits alternating with shales	20 ft. +
	Fferam Shales	Dark Blue shales	60 ft.
	Fferam Ironstone	Ironstone and ferriferous grit	20–40 ft.

The ironstone and succeeding shales are also exposed in an old quarry south of Llanbabo (Greenly 1919 : 543), and graptolites of the *N. gracilis* zone were obtained from the shales in both areas by Greenly and his collectors.

The Llanbabo Church Grits are best exposed in the old quarry 100 yds. south-west of the church, where 20 ft. of strata are exposed, pebbly graded grit beds up to 2 ft. thick alternating with silty blue-grey shales. The latter contain a graptolite fauna, regarded by Elles (in Greenly 1919 : 455) as being high in the *N. gracilis* zone, above the Fferam Shales. The grits contain a shelly fauna, mainly of disarticulated brachiopod valves, which correlates well with the Tandinas Shales at Careg-onen, and with the Derfel Limestone of the Arenig area (Whittington & Williams, 1955): *Orthambonites* (?) sp. (2), *Nicolella humilis* Williams, *Cyrtonotella* sp. (1), *Dolerorthis* cf. *tenuicostata* Williams, *Platystrophia precedens major* Williams, *Ptychopleurella* sp. (2), *Plaesiomys* (*Dinorthis*) sp., *Salopia salteri gracilis* Williams, *Onniella*(?) sp., *Horderleyella*(?) sp., *Kullervo* aff. *panderi* Öpik, *Clitambonites*(?) sp., *Ilmarinia* sp., *Palaeostrophomena* sp., *Eoplectodonta lenis* Williams, *Leptaena*(?) sp., *Echinosphaerites* sp.

The Llanbabo Church Grits are also exposed at Fferam-uchaf, in the north-east corner of the field immediately east of the farmhouse (Greenly 1919 : 451 and outcrop labelled 'conglm.' in fig. 207), with a similar fauna: *Orthambonites* (?) sp., *Platystrophia*(?) sp., *Ptychopleurella* sp. (2), *Plaesiomys* sp., *Dolerorthis*(?) sp., *Salopia*(?) sp., *Bilobia* aff. *musca* Öpik, *Leptestiina* sp., *Eoplectodonta lenis* Williams, *Leptaena* sp.

Above the basal Caradoc rocks of the *N. gracilis* zone are shales, poorly exposed and of uncertain extent. Greenly (1919 : 454–455) records graptolites from the zones of *Cl. wilsoni* and *Dicranograptus clingani*, from shales at Llanbabo which probably rest on the Llanbabo Church Grits. There is no evidence of the thickness of these zones, or of their relation one to another, though the close proximity of the outcrops to the older Caradocian rocks suggests that the zones are not very thick.

In the Eilian sector no fossils have been found to add to Greenly's collection (1919 : 466), which contains *Glyptograptus teretiusculus* (Hisinger) and *Placoparia* sp. The section seen on the shore between the Carmel Head Thrust at Porth-y-corwgl and the gneisses south of Porth-y-gwichiaid contains a number of units, separated by faults. Between Porth-y-corwgl and Fresh Water Bay are a series of conglomerates, pebbly grits and shales (the Fresh Water Bay Group), all apparently younging south and overturned. Between Ogof Fach and Ogof Fawr are highly cleaved and sheared grey shales, intruded by acid sills. On the northern side of Porth-y-gwichiaid are fine siltstones and mudstones, with some worm burrows, also cleaved and folded; it is not known in which direction they young. On the south side of the Porth is a series of siltstones, shales, conglomerates and an ironstone, partly slumped in some horizons, and disposed in a complex syncline.

(e) *The Gynfor Outliers*

On the north coast the Ordovician rocks are exposed in a number of faulted and folded outliers resting on the Mona Complex. Two groups are present, separated by a disconformity. The earlier (Porth Wen Group), of Arenig Age, is of two conglomerate and grit formations, the lower being a purple conglomerate (the Hell's Mouth Conglomerate), absent from some exposures, and the upper a pale brown weathering sequence of conglomerates, grits and sandstones containing an Arenig fauna (the Torllwyn Formation). Brachiopods were obtained from some of the localities listed by Greenly (1919 : 469–470):

(i) 10 ft. above the unconformity on the north side of Ogof Gynfor (exposure in Greenly *op. cit.*, Pl. XXIX): *Rhynchorthis rotundus* gen. et sp. nov., *Estlandia*(?) sp.

(ii) about 40 ft. above the unconformity, 45 yds. north of the last locality, north of the faulted syncline containing Gynfor Shales in the core: *Lenorthis* sp., *Hesperonomiella*(?) sp., *Monorthis* sp., *Panderina* cf. *lamellosa* sp. nov., *Pleurorthis* sp., *Skenidioides* sp., *Rhynchorthis* sp., *Tritoechia* sp., *Antigonambonites* sp., *Inversella* (*Reinversella*?) sp., *Ahtiella quadrata* sp. nov., crinoid ossicles, polyzoan fragments.

(iii) Thirty to forty ft. above the unconformity, on the north side of the ridge of Mynydd-pant-y-gaseg, 85 ft. east of the summit: *Orthambonites*(?) sp., *Ahtiella*(?) sp. (poorly preserved).

(iv) in the cutting of the Graig Wen tramway, 70 yds. below the winding house, collected from loose material: *Lenorthis* cf. *proava* (Salter), *Panderina*(?) sp., *Rhynchorthis*(?) sp., *Antigonambonites*(?) sp.

The specimens of *Lenorthis* examined include a number from the Geological Survey collection (Z1470–1502).

The upper group (Llanbadrig Group) is Caradoc in age, with an ascending sequence of cherty shales (Gynfor Shales), an ironstone (Penterfyn Ironstone) and shales and ferriferous grits (Porth Pridd Formation). Faunas of graptolites from the lower and upper formations (Greenly 1919 : 470–471) come from the *N. gracilis* zone, and hence (it is unlikely that the Arenig fossils are derived) there must be a plane of disconformity within the Torllwyn Formation or at its top. Erosion surfaces are present within it, and the contact with the shales above is also abrupt, with the shales resting on a slightly irregular surface of coarse conglomerate.

The Silurian shales of Parys Mountain lie above the volcanic Parys Group but the nature of the contact between them is unknown. Greenly (1919 : 481–482) lists graptolite faunas from all the Llandovery zones. There is no palaeontological evidence for Silurian rocks at Rhos-mynach (Greenly 1919 : 482–483), and the shales there are intercalated between rhyolites which are probably equivalent to the Parys Group.

(f) *Faunal Lists*

Explanation of symbols: ex. = *Didymograptus extensus* Zone; hi. = *D. hirundo* Zone; bi. = *D. bifidus* Zone; mu. = *D. murchisoni* Zone; te. = *Glyptograptus teretiusculus* Zone; gr. = *Nemagraptus gracilis* Zone.

BRACHIOPODA

	ex.	hi.	bi.	mu.	te.	gr.
Ahtiella concava sp. nov.	—	—	×	—	—	—
Ahtiella quadrata sp. nov.	—	×	—	—	—	—
Antigonambonites pyramidalis sp. nov.	—	×	—	—	—	—
Apomatella(?) sp.	—	—	×	—	—	—
Bilobia aff. *musca* (Öpik)	—	—	—	—	—	×
Camerella sp.	—	—	—	—	—	× ?
Clitambonites(?) sp.	—	—	—	—	—	×
Cyrtonotella sp. (1)	—	—	—	—	—	×

	ex.	hi.	bi.	mu.	te.	gr.
Cyrtonotella sp. (2)	—	—	—	—	—	× ?
Dactylogonia sp.	—	—	×	—	—	—
Dalmanella(?) sp.	—	—	—	—	—	×
Dolerorthis cf. tenuicostata Williams	—	—	—	—	—	×
Eoplectodonta lenis Williams	—	—	—	—	—	×
Estlandia(?) sp.	—	×	—	—	—	—
Harknessella(?) sp.	—	—	—	—	—	×
Hesperonomiella carmelensis sp. nov.	×	× ?	—	—	—	—
Horderleyella(?) sp.	—	—	—	—	—	×
Ilmarinia sp.	—	—	—	—	—	×
Kiaeromena(?) sp.	—	—	—	—	—	× ?
Kullervo aff. *panderi* (Öpik)	—	—	—	—	—	×
Lenorthis proava (Salter)	×	×	—	—	—	—
Lenorthis sp.	—	—	×	—	—	—
Leptaena sp.	—	—	—	—	—	×
Leptestiina derfelensis (Jones)	—	—	—	—	—	×
Metacamerella cf. *balcletchiensis* (Davidson)	—	—	—	—	—	× ?
Monorthis typis gen. et sp. nov.	—	×	—	—	—	—
Nicolella humilis Williams	—	—	—	—	—	×
Onniella(?) sp.	—	—	—	—	—	×
Orthambonites(?) sp. (1)	—	—	×	—	—	—
Orthambonites(?) sp. (2)	—	—	—	—	—	×
Palaeostrophomena sp.	—	—	—	—	—	×
Palaeostrophomena(?) sp.	—	—	—	—	—	× ?
Panderina lamellosa sp. nov.	—	×	× ?	—	—	—
Paurorthis(?) sp.	—	—	×	—	—	—
Plaesiomys sp.	—	—	—	—	—	×
Plaesiomys cf. *robusta* (Bancroft)	—	—	—	—	—	×
Plaesiomys (*Dinorthis*) sp.	—	—	—	—	—	×
Platystrophia precedens major Williams	—	—	—	—	—	×
Plectorthis(?) sp.	—	—	×	—	—	—
Pleurorthis costatus sp. nov.	—	×	—	—	—	—
Porambonites (s.s.) sp.	—	×	—	—	—	—
Ptychoglyptus sp.	—	—	—	—	—	× ?
Ptychopleurella sp. (1)	—	—	×	—	—	—
Ptychopleurella sp. (2)	—	—	—	—	—	×
Rectotrophia globularis gen. et sp. nov.	—	×	—	—	—	—
Reinversella monensis gen. et sp. nov.	—	×	—	—	—	—
Rhynchorthis rotundus gen. et sp. nov.	—	×	×	—	—	—
Salopia salteri gracilis Williams	—	—	—	—	—	×
Sericoidea abdita Williams	—	—	—	—	—	×
Skenidioides sp. (1)	—	×	—	—	—	—
Skenidioides sp. (2)	—	—	×	—	—	—
Tritoechia sp.	—	×	—	—	—	—

TRILOBITA

Amphilichas sp. (1)	—	—	—	—	—	× ?
Amphilichas sp. (2)	—	—	—	—	—	×
Ampyx sp. (1)	×	—	—	—	—	—
Ampyx sp. (2)	—	—	—	—	—	×
Bergamia(?) sp.	—	—	×	—	—	—
Calymenid	—	—	—	—	—	× ?

	ex.	hi.	bi.	mu.	te.	gr.
Ceraurinella sp.	—	—	—	—	—	× ?
Illaenus sp.	—	—	—	—	—	× ?
Monella perplexa gen. et sp. nov.	×	× ?	—	—	—	—
Neseuretus monensis (Shirley)	×	—	—	—	—	—
Ogygiocaris selwynii (Salter)	×	—	—	—	—	—
Placoparia sp.	—	—	—	—	× ?	—
Pliomerops sp.	—	—	—	—	—	× ?
Protobronteus greenlyi sp. nov.	—	—	—	—	—	× ?
Selenoharpes(?) sp.	—	—	—	—	—	× ?
Sphaerexochus sp.	—	—	—	—	—	×
Stenopareia sp.	—	—	—	—	—	× ?

III. FAUNAL AFFINITIES AND CORRELATIONS

The basal rocks of the Principal Area, the Carmel Formation, have a fauna characterized by few species, but a large number of individuals, especially *Lenorthis proava* (Salter), which occurs in vast numbers as disarticulated valves. Similar species are found elsewhere in Wales at this horizon, at Arenig in the Henllan Ash, and at St. David's and the Carmarthen-Whitland region. In the latter regions they are described as *Orthis carausii* Salter, and are associated with *Lenorthis alata* (Salter). *Ogygiocaris selwynii* (Salter) and *Neseuretus monensis* (Shirley), which are found sporadically, belong to genera which are widespread throughout Wales at this time. *Monella perplexa* gen. et sp. nov. is at present cryptogenic, but may be a survivor of the Cambrian *Corynexochida.*

Hesperonomiella carmelensis sp. nov. belongs to a genus described by Ulrich & Cooper (1938) from the upper Canadian (approximately upper Llanvirn) of much of North America. The genus is described as having chilidial plates, but in some cases they are very rudimentarily developed, and in this species are not developed at all. It is possible that later species of *Hesperonomiella* and its ally *Hesperonomia* have their origin in forms comparable with this species.

Near the base of the overlying Treiorwerth Formation, and at the base of the system along the Berw Fault is a rich shelly fauna, consisting almost wholly of brachiopods. Three stocks, *Lenorthis proava*, *Hesperonomiella carmelensis*, and *Monella*(?) sp. persist from the Carmel Formation, but are joined by a variety of forms, some new, some with American affinities, and some very similar to contemporary Baltic faunas. *Rhynchorthis rotundus* gen. et sp. nov., *Porambonites* sp. and *Antigonambonites pyramidalis* sp. nov. are closely related to contemporary Baltic stocks (Alichova 1953, Table 1). *Porambonites* and *Antigonambonites* appear similar in morphological grade to the earliest Russian species (of $B_1\beta$ in Estonia, o_1v_1 on the Russian platform) and one can correlate the Anglesey fauna with confidence with this horizon. *Rhynchorthis* is similar to *Angusticardinia*, also from this level, but appears to be more primitive in its features. *Panderina lamellosa* is more advanced than contemporary Russian species, again from this horizon. *Reinversella monensis* gen. et sp. nov. is closely related to *Inversella* Öpik from Estonia and Norway, a later genus from the upper Arenig (B_{III} and later) (Öpik 1933 : 23). *Ahtiella quadrata* sp. nov., is a member of a genus which is also found later in the Baltic region (B_{111}–C_1). It is thus probable that the two faunas were closely linked at this time with migration possible in either direction.

The stocks with American affinities, *Pleurorthis costatus* sp. nov. and *Tritoechia* sp., differ markedly from those just described. In America *Pleurorthis* is known from the much later Mystic conglomerate of Quebec and the Table Head Series of Newfoundland (both upper Llanvirn), with rather different species (Cooper 1956 : 330–333). *Tritoechia* ranges throughout the Arenig equivalents in North America (much of the Canadian of Twenhofel *et al.*, 1954, chart 2).

Monorthis typis gen. et sp. nov. is of uncertain affinities, and makes its only known appearance in this fauna. *Skenidioides* can probably best be regarded as indigenous, as it occurs in the Mytton Flags of Shropshire and at Tourmakeady, Co. Mayo (Professor A. Williams, personal communication), and is also present in the Whitland region. *Rectotrophia globularis* gen. et sp. nov. has affinities with both American and Bohemian forms. *Matherella,* a sinistral gastropod, belongs to a small but widespread group of shells, with both American and Bohemian members.

Llanvirn shelly faunas are sparse, as the sediments are predominantly shaley. *Orthambonites*(?) sp. (1) may be regarded as indigenous, being closely related to *Lenorthis*, as may *Skenidioides* sp. (2) descended from the Arenig species. *Ahtiella concava* sp. nov. either is descended from the Arenig species, or is a later migrant from the Baltic region. *Ptychopleurella* sp. (1) is an atypical member of the genus, possibly earlier than any of the American species. Trinucleids make their appearance in Anglesey at this time, but are indigenous south British elements which have been recorded widely within Wales (Whittard 1955–64; Whittington 1966), and may well have reached Anglesey earlier than this time.

The dominant shelly fauna taken from rocks belonging to the *Nemagraptus gracilis* Zone is closely comparable with that found at Derfel, near Arenig (the Derfel Limestone fauna of Whittington & Williams 1955), which has been divided into a native association of elements known in Wales from older rocks, together with stocks which migrated from the east Baltic, Russia, Bohemia and the North Atlantic Province. As developed in Anglesey the fauna has similar elements. Native stocks include *Orthambonites* (?) sp. (2), *Ptychopleurella* sp. (2), *Dinorthis* sp., *Eoplectodonta lenis* Williams, *Sericoidea abdita* Williams, *Salopia salteri gracilis* Williams, *Onniella*(?) sp., *Horderleyella* sp., *Amphilichas* sp. (2), *Ampyx* sp. (2), and trinucleids. Elements regarded by Whittington & Williams as exotic include *Nicolella humilis* Williams, *Cyrtonotella* sp., *Dolerorthis* cf. *tenuicostata* Williams, *Platystrophia precedens major* Williams, *Palaeostrophomena* sp., *Leptaena* sp., *Leptestiina derfelensis* (Jones) and *Kullervo* aff. *panderi* Öpik. Other stocks occurring in Anglesey, but not so far found at Derfel, provide further evidence of the Baltic affinities of the fauna. *Bilobia* aff. *musca* Öpik has strong affinities with Öpik's species, from this horizon in the east Baltic. *Ilmarinia* sp. and *Clitambonites*(?) sp. also belong to Baltic genera, though *Ilmarinia* occurs at a higher horizon in the east. In the light of the affinities of the Arenig faunas discussed above, the Derfel Limestone fauna is best regarded, not as an invasion of the region by an entirely new fauna during the *N. gracilis* transgression, but as the continuation of an association which existed in the lower Ordovician.

The fauna of the limestone blocks in the Garn Breccia at Porth Padrig is not younger than the *N. gracilis* Zone, and may be older. The trilobites of the limestone are similar to those of the Derfel Limestone, *Ceraurinella*, *Amphilichas* and *Illaenus* being common to both. Other trilobites in the fauna are *Selenoharpes*(?) sp., a calymenid, *Piomerops* sp. and *Protobronteus greenlyi* sp. nov. All these may be traced to the north Atlantic province, to which Whittington attributes *Ceraurinella*(?), *Illaenus* (s.l.) and *Harpes* (s.l.) from the Derfel Limestone. The brachiopods of the fauna are more ambiguous. *Palaeostrophomena*(?) sp., *Cyrtonotella* sp., and *Kiaeromena*(?) sp. have Baltic affinities, and the genera occur in the Derfel Limestone. *Ptychoglyptus* is known from slightly higher horizons in Norway (4b or the *Climacograptus peltifer* zone; Spjeldnaes 1957 : 61), and from the Girvan area in Scotland (Williams 1962 : 193). *Camerella* and *Metacamerella* are both found in Scotland and America. Thus these latter three brachiopod genera, together with the trilobites, may indicate an intermingling of the Baltic and Scoto-Appalachian faunas, at least in the limestone facies, if not in the grits at Llanbabo or in the Careg-onen and Derfel sediments. It appears likely, from lithological evidence, that the source area of limestone deposition lay to the north of Anglesey, but probably still on the upfaulted Irish Sea Landmass.

The specimens examined either come from Greenly's collection or were collected by the author. Those with numbers prefixed by 'BB' (brachiopods) or 'In' (trilobites) have been donated to the British Museum (Natural History). Greenly's collection is now in the possession of the Geological Survey, and the specimen numbers bear the prefix 'Af'.

IV. SYSTEMATIC DESCRIPTION OF THE BRACHIOPODA

Order ORTHIDA Schuchert & Cooper 1932

Suborder ORTHIDINA Schuchert & Cooper 1932

Superfamily **ORTHACEA** Woodward 1852

Family **HESPERONOMIIDAE** Ulrich & Cooper 1936

Genus ***HESPERONOMIELLA*** Ulrich & Cooper 1936

***Hesperonomiella carmelensis* sp. nov.**

(Pl. 1, figs. 1–6)

1919 *Rafinesquina* cf. *llandeiloensis* (Davidson); Matley *in* Greenly : 142.

Diagnosis. Semicircular to subquadrate *Hesperonomiella* about three-quarters as long as wide, hinge line equal to the greatest width, cardinal angles about 80–85°; valves subequally and gently convex, lateral and anterior commissures plane; pedicle valve slightly carinate with convex lateral flanks, interarea wide, plane, apsacline, delthyrium open, width at teeth one-quarter the width of the valve; brachial valve with shallow rounded sulcus dying out anteriorly, interarea wide, shorter than the ventral one, anacline, notothyrium wide and open; neither umbo incurved; ornament finely and unequally multicostellate, costellae flat-topped with narrow interspaces, numbering thirty per 5 mm. at 5 mm. from the umbo, arising by bifurcation, every fifth or sixth costella more prominent; teeth triangular, dental lamellae widely divergent forwards and slightly divergent to the floor of the valve, short but not receding, continued as low ridges around the muscle scars; muscle scars triangular in outline and relatively confined to the delthyrium, in length one-quarter that of the valve, adductor and diductor scars expanding forwards and equal in length; median trunks of the *vascula media* slightly impressed, converging forwards from the ends of the diductor scars to come in contact at half the length of the valve and then diverging again; cardinal process a simple lenticular septum with low lateral ridges parallel to its posterior half; brachiophores diverging at 80°, short and triangular in cross section, ends bevelled, largely adpressed to the valve surface; muscle scars and mantle canals not seen; subperipheral rim present.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	Internal mould of brachial valve (BB.30529)	17·6	24·4
Paratypes.	Internal mould of pedicle valve (BB.30530)	19·6	—
	Internal mould of pedicle valve (BB.30531)	19·2	26·9
	Internal and external moulds of pedicle valve (BB.30532a–b)	—	—
	External mould of brachial valve (BB.30533)	19·3	—

Horizon and locality. Carmel Formation, sandstone 50 yds. north-east of Prys-owain-bach, Carmel. N.G.R. 38878282.

Discussion. Although the family Hesperonomiidae as erected by Ulrich & Cooper (1938 : 114) was defined as comprising forms with a chilidium, some of the species described by them have only rudimentary chilidial plates, which may be interpreted as a thickening of the inner edge of the interareas, and a swelling of the brachiophores (cf. Ulrich & Cooper 1938, Pl. 19, figs. 9, 10, 14, 17). Two genera were described, *Hesperonomia* with plano- or concavo-convex valves, and *Hesperonomiella* with gently biconvex valves. The new species therefore belongs in the latter genus. All the described species have a uniform ornament, whereas the new species is unequally parvicostellate. Internally the closest species is *Hesperonomia louisensis* Ulrich & Cooper, from the Sarbach formation, Alberta (Ulrich & Cooper 1938 : 120), which has almost identical ventral musculature and dorsal cardinalia, but has a concave brachial valve and equally parvicostellate ornament.

The specimens from the type locality are all very uniform in size, and to some extent distorted. The smallest pedicle valve had a length of 9·1 mm., and in a sample of eleven pedicle valves the average length was 16·6 mm., with a variance of 4·42, suggesting that the sample was current drifted with good sorting.

Genus ***MONORTHIS*** nov.

DIAGNOSIS. Quadrate shells, widest at a long straight hinge line, alate, with slightly acute cardinal angles; lateral profile flatly biconvex, with very low pyramidal pedicle valve and evenly convex brachial valve; pedicle valve with a low carinate fold with plane flanks, the rest of the surface evenly convex, almost flat; brachial valve with a deep rounded sulcus, swollen folds on either side of it, and concave lateral margins; lateral commissure flat, anterior commissure uniplicate; ventral interarea short and wide, apsacline to almost catacline, delthyrium open, dorsal interarea shorter, anacline, notothyrium open; surface finely multicostellate.

Ventral interior with receding dental lamellae, teeth and musculature not seen.

Dorsal interior with elevated notothyrial cavity; cardinal process a thin ridge; brachiophores thin and short, supported by a mass of callus, sockets thin and deep; adductor scars not seen but separated by a large median ridge corresponding to the exterior sulcus.

TYPE SPECIES. *Monorthis typis* sp. nov. from the Treiorwerth Formation.

DISCUSSION. The simple cardinalia in the brachial valve, together with the transverse shape and the convexity of valves, form the distinctive features of the genus. *Metorthis* Wang is similar in shape, but has a thickened cardinal process and muscle scars like those of *Dinorthis*, whereas this genus seems to have the confined muscle scars of *Orthis*. The genus is tentatively placed in the *Hesperonomiidae*, since it agrees with the diagnosis of that family (Ulrich & Cooper 1938 : 114) except that neither chilidial plates nor a chilidium are present. The structure interpreted by Ulrich & Cooper as chilidial plates may be no more than the thickening of the inner edge of the interarea where it forms the posterior part of the brachiophores.

Monorthis typis gen. et sp. nov.

(Pl. 1, figs. 7–13)

1919 *Orthis* (*Hebertella*) *vespertilio* J. de C. Sowerby; Matley *in* Greenly : 442.

DIAGNOSIS. Quadrate biconvex *Monorthis*, widest at a long straight hinge-line, alate, with slightly acute cardinal angles; lateral profile flatly biconvex, with very low pyramidal pedicle valve and an evenly convex brachial valve; pedicle valve with a low carinate fold with plane flanks, the rest of the surface evenly convex, almost flat, interarea short and wide, apsacline to almost catacline, delthyrium open; brachial valve with a deep rounded sulcus, swollen folds flanking it, and concave lateral margins, interarea shorter than the ventral one, anacline, notothyrium open; surface of both valves finely multicostellate, costellae numbering four per mm. at the shell margins but everywhere poorly preserved; ventral interior with receding dental lamellae, teeth not seen; musculature not seen but probably confined; low ridges marking the sides of the fold are aligned with the dental lamellae; dorsal interior with small elevated notothyrial platform; cardinal process a thin ridge; brachiophores short and thin, supported by a mass of callus cementing them to the sides of the notothyrial cavity; sockets thin and deep; adductor scars probably small, and separated by a large median elevation corresponding to the exterior sulcus.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	Internal mould of brachial valve (BB.30534)	7·1	—
Paratypes.	Internal and external mould of brachial valve (BB.30535a–b) . . .	6·9	—
	Internal and external moulds of pedicle valve (BB.30536a–b) . . .	7·1	11·0

Type horizon and locality. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

Discussion. The new species is generically distinct from other known orthaceans, and can be distinguished by features referred to in the generic description from various hesperonomiids with which it is most closely related. The poor preservation of the valves makes it impossible to carry out any analysis of the ribbing or of the various dimensions, except to remark that the average percentage length of five brachial valves relative to width was 62·6 (range 55·3–73·4).

Family **ORTHIDAE** Woodward 1852

Subfamily **ORTHINAE**

Genus ***CYRTONOTELLA*** Schuchert & Cooper 1931

Cyrtonotella sp. (1)

(Pl. 2, figs. 9, 10, 13)

Figured specimen (measurements in mm.)

	Length	Width
Internal and external mould of brachial valve (BB.30521a–b)	—	—

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. Two valves have been found, one being very incomplete, the other a brachial valve in fair condition. It is semi-circular, with a slight sulcus. The hinge-line is straight, with an anacline interarea and probably an open notothyrium. The ornament is multicostellate; the margin has more than forty ribs but the details of the branching are obscure. Internally the cardinal process is simple and continuous with a median septum, the brachiophores are orthoid, diverging at 80°, and the sockets are elongated parallel to the hinge-line. These characters agree well with those of the brachial valve figured by Williams (*in* Whittington & Williams 1955, pl. 38, figs. 14–16), and referred to *Cyrtonotella* aff. *kukersiana* (Wysogorski).

Cyrtonotella sp. (2)

(P.. 2, figs. 14–16)

Figured specimens (measurements in mm.)

	Length	Width
Exterior of incomplete pedicle valve (BB.30522) .	7·9	—
Exterior of incomplete brachial valve (BB.30523) .	13·5	—
External mould of incomplete brachial valve (BB.30524)	8·9	—

Horizon and locality. Garn Formation, Limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The valves have the external features of *Cyrtonotella*, but the interareas and the internal features are concealed. The pedicle valve is strongly convex, and is probably semi-circular in outline with a straight, slightly alate hinge-line; the interarea cannot be very long. The brachial valve is gently concave, with a slight median sulcus in one specimen (BB.30524). The ornament of both valves is slightly fascicostellate, with seven to twelve costellae per 5 mm. antero-medianly, and the interspaces have closely spaced fine growth lines. The pattern of the branching of the ribs cannot be made out. Owing to the incompleteness of the valves it is not possible to compare them closely with any other species.

Genus ***LENORTHIS*** Andreeva 1955

Lenorthis proava (Salter)

(Pl. 1, fig. 21; Pl. 2, figs. 1–8)

1866 *Orthis calligramma* var. *proava* Salter: Appendix 335–336, pl. 22, fig. 1.
1868 *Orthis Carausii* (Salter ms.); Davidson : 315, pl. 16, fig. 23.
1869 *Orthis Carausii* (Salter ms.); Davidson : 229, pl. 33, figs 1–7.
1869 *Orthis calligramma* var. *proava* Salter; Davidson : 241, pl. 35, figs. 13–15.
1883 *Orthis carausii* Salter; Davidson: 182–184, pl. 14, figs. 21–26.
1912 *Orthis proava* Salter; Matley : 78–79.

Diagnosis. Subquadrate biconvex *Lenorthis* five-sixths as long as wide and one-third as deep as wide, the pedicle valve being twice as deep as the brachial valve; widest at the hinge line, with cardinal angles of approximately 90°, anterior and lateral commissures plane; pedicle valve convex, slightly carinate, interarea curved, apsacline, one-sixth the length of the valve; brachial valve gently convex with a shallow rounded median sulcus and concave flanks, interarea anacline, shorter than the ventral one; ornament of simple rounded costae with equal rounded interspaces, numbering sixteen to twenty, with a wave-length of 0·93 mm. at 5 mm. from the dorsal umbo, the pedicle valve bearing a median costa and the brachial valve four costae in the sulcus; costae covered by fine filae, growth lines rarely seen except at the margins of adult shells; ventral interior with blunt triangular teeth and small crural fossettes; dental lamellae vertical, receding; muscle scars confined to the delthyrium but details not seen, width three-twentieths that of the valve, length length unknown; dorsal interior with thick median septum running half the length of the valve; adductor scars quadripartite, on either side of the septum, occupying four-tenths the width of the valve; margins of both valves crenulated.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal mould of brachial valve (BB.30512) .	10·5	15·1
Internal and external moulds of pedicle valve (BB.30513a–b)	11·7	15·8
Internal mould of pedicle valve (BB.30514) . .	distorted	
Internal and external moulds of brachial valve (BB.30515a–b)	11·0	—
Internal mould of pedicle valve (Af.1337) . .	11·4	15·0

HORIZON AND LOCALITIES. Carmel Formation, sandstones, 50 yds. north-east of Prys-owain-bach cottage, Carmel. N.G.R. 38878283. Specimen Af.1337 is from the same horizon, 130 yds. north-west of Ty-hen, Treiorwerth. N.G.R. 35567872.

DISCUSSION. The specimens of *L. proava* from all the localities in the Carmel Grits are preserved in a coarse sandstone, so that the finer detail of the ornament and of the mantle canal patterns is lost. It is seldom possible to count all the costae, since the finer ribs close to the hinge line are not preserved, and the anterior border of the ventral muscle scars is not seen. These scars may be triangular in shape, with the adductors not enclosed by the diductors and equal in length to them. In ten brachial valves the costae 5 mm. anteromedianly from the umbo have a mean wavelength of 0·93 mm. (var 0·0141). In the interior of the brachial valve the anterior and posterior adductor scars are equal in area, the posterior pair deeply sunk beneath the notothyrial platform. The brachiophores are closely adpressed to the edges of the platform, and the ends are bevelled.

The majority of the figured specimens come from Prys-owain-bach, as here the species may be found in greatest abundance, and without much distortion. When first described by Salter, the locality was given as 'grits among the black shales of Llanerchymedd, Anglesey' (1866 : 336). No type locality is given for the figured specimens, which have since been lost. Earlier in the same work (259) the species, as *Orthis calligramma* var., is listed as occurring at a locality one mile north-west of Llanerchymedd, at Treiorwerth, and at Tyn-twr, 4 miles south of Llangefni. The first of these localities cannot easily be located, and good specimens are not found in that region; the second locality is that listed above at Ty-hen.

TABLE 1

	(a)	(b)
$\bar{l}$ (var. l)	10·36 (5·017)	9·44 (2·600)
$\bar{w}$ (var. w)	12·12 (5·438)	12·70 (3·736)
r	0·753	0·787
a (var. a)	1·041 (0·01339)	1·199 (0·01092)
a (var. b)	1·34 (1·513)	1·38 (1·0054)

TABLE 1. Statistics of length (l) and width (w) of (a) thirty-five pedicle valves and (b) fifty brachial valves of *Lenorthis proava* (Salter) from sandstones 50 yds. north-east of Prys-owain-bach, Carmel.

Lenorthis sp.

(Pl. 2, figs. 11–12)

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30601a) .	—	—
Internal mould of brachial valve (BB.30602) .	11·7	14·6 (est.)

HORIZON AND LOCALITY. Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach cottage, Bod Deiniol. N.G.R. 37688528.

DISCUSSION. The species is very similar to *Lenorthis proava*, and is probably closely related. The ratio of length to width of the brachial valve is very similar; in five valves the mean length is 9·56 mm. and width 12·68 mm. There may, however, be more costae, as at least twenty-four can be counted in some specimens, and their wavelength 5 mm. from the umbo in the brachial valves is approximately 0·75 mm. compared with 0·95 mm. in *L. proava*.

Genus ***ORTHAMBONITES*** Pander 1830

Orthambonites (?) sp. (1)

(Pl. 1, figs. 14, 16, 17)

1919 *Orthis* cf. *proava* Salter; Matley *in* Greenly : 452.

FIGURED SPECIMEN (measurements in mm.)

	Length	Width
Internal and external moulds of brachial valve (Af.1398–9)	6·9	—

HORIZON AND LOCALITY. Nantannog Formation, gritty shales by well on the west side of the road, 220 yds. west of Fferam-uchaf. N.G.R. 36188667.

DISCUSSION. The valve has about twenty rounded costae, with late internal and external bifurcations, and with fine parvicostellae in the interspaces. In shape the valve is semicircular, with rounded cardinal angles and the greatest width just anterior to them, gently convex and slightly sulcate. The internal details are similar to those of *Lenorthis proava* (Salter). Division of the costae is described by Cooper (1956) in two species, *O. bifurcatus* and *O. divaricatus*. The latter species, with its few late bifurcations, is very similar.

Orthambonites (?) sp. (2)

(Pl. 1, figs. 15, 18–20)

DESCRIPTION. Small subcircular *Orthambonites* or *Lenorthis* with the more convex pedicle valve four-fifths as long as wide and one quarter as deep as long, ornamented by about seventeen rounded costae with a wavelength of 0·7 mm. at 5 mm. from the ventral umbo.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30510) . .	10·7	12·0
Internal and external moulds of pedicle valve (BB.30511a–b)	4·9	6·3

HORIZON AND LOCALITY. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

DISCUSSION. A few pedicle valves of *Orthambonites*(?) have been found from the Llanbabo Grits, together with a few fragmentary brachial valves. The numbers found are too few to analyse statistically, the mean length and width of three pedicle valves being 8·7 mm. and 10·1 mm. respectively. The species recalls *O. parvicrassicostatus* Cooper, from the Caradoc of the Girvan area (Williams 1962 : 98), which has about nineteen costae on the pedicle valve, angular in cross section. Neither this species nor the preceding one can be definitely assigned to *Orthambonites*, since the course of the *vascula media* has not been observed.

Genus ***PLEURORTHIS*** Cooper 1956

Pleurorthis costatus sp. nov.

(Pl. 2, figs. 17–19; Pl. 3, figs. 1–4, 6)

DIAGNOSIS. Subequally biconvex, transverse, subquadrate to semicircular *Pleurorthis*, length seven-tenths the maximum width, which is at or just anterior to the hinge-line; cardinal angles rounded to slightly acute; lateral commissures almost straight, anterior commissure uniplicate; pedicle valve initially with a median fold, reversing to form a sulcus with gently curved flanks at about 3–4 mm. from the umbo; ventral interarea slightly curved, apsacline, about one-fifth the length of the valve; brachial valve initially with a slight sulcus, reversing to form a fold corresponding to the ventral sulcus, interarea wide, anacline, shorter than the ventral one, notothyrium open; ornament on both valves of sharp angular costae, about ten being primary, increasing by bifurcation and numbering about eight per 5 mm. antero-medianly at 5 mm. from the umbo, growth lines not seen; in ventral interior teeth blunt, triangular, dental lamellae descending vertically to the floor of the valve and slightly receding, diverging anteriorly at 70°; muscle scars largely confined to the delthyrial cavity, elevated on a callosity ending anteriorly in a blunt forward pointing 'V'; adductor track equal in width to one diductor scar, both sets of scars expanding forwards; *vascula media* trunks parallel and submedian; in dorsal interior notothyrial platform low, one-sixth the width of the valve; cardinal process a simple ridge; brachiophores blade-like, diverging from each other at more than 90°, supported only by the notothyrial platform; sockets are pits just below the hinge-line; adductor scars extend to the midlength of the valve, separated by a median ridge of the same length, the posterior pair the smaller, wider than long, anterior pair triangular, coming to a blunt point close to the ridge; costellae impressed on the inner surface of young valves.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	Internal mould of brachial valve (BB.30516)	10·5	19·9
Paratypes.	Internal and external moulds of pedicle valve (BB.30517a–b) . . .	10·8	—
	Internal mould of pedicle valve (BB.30518)	12·0	—
	Internal and external moulds of brachial valve (BB.30555a–b) . . .	7·9	—

Type horizon and locality. Treiorwerth Formation, sandstones, 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

Discussion. The new species conforms to the generic diagnosis of *Pleurorthis*, but differs markedly from the species described by Cooper (1956 : 329–333). The ornament is much more coarsely costellate than even the coarsest described by him, the development of fold and sulcus is much more pronounced, and internally the described species have no excessive development of secondary calcite in the larger shells. This last trend in the new species gives rise to a pseudospondylium, and leads to the obliteration of all internal impressions of the costellae.

Table 2

	(a)	(b)
$\bar{l}$ (var. l)	8·56 (3·433)	7·55 (2·891)
$\bar{w}$ (var. w)	12·26 (5·610)	11·40 (6·181)
r	0·867	0·842
a (var. a)	1·124 (0·00653)	1·462 (0·01152)
b (var. b)	2·639 (0·5091)	0·368 (0·6392)

Table 2. Statistics of length (l) and width (w) of (a) forty-eight pedicle valves, and (b) fifty-four brachial valves of *Pleurorthis costatus* sp. nov. from sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

Subfamily **PRODUCTORTHINAE** Schuchert & Cooper 1931

Genus ***NICOLELLA*** Reed 1917

Nicolella humilis Williams

(Pl. 3, figs. 5, 7–9)

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of brachial valve (BB.30519a–b)	10·5	18·4 (est.)
Internal and external moulds of brachial valve (BB.30520a–b)	10·1	—

HORIZON AND LOCALITY. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

DISCUSSION. Specimen BB.30520 has, as far as can be seen, an identical ribbing pattern to that of *N. humilis*, with possibly eighteen primary costae, though no secondary costae are developed, because of the small size of the valve. BB.30519 is also referred to this species; there appear to be only fourteen primary costae, allowing for state of preservation, and internal and external secondary costae originate at 5·6 mm from the umbo.

Genus ***PANDERINA*** Schuchert & Cooper 1931

Panderina lamellosa sp. nov.

(Pl. 3, figs. 10–18)

DIAGNOSIS. A species of *Panderina* with semicircular alate valves, three-quarters as long as wide, the pedicle valve with the greater convexity, evenly convex medianly with concave lateral flanks; the brachial valve gently convex with a shallow sulcus, narrow posteriorly but rapidly widening; anterior commissure slightly uniplicate; radial ornament of low rounded costellae arising by implantation, crossed by imbricate growth lamellae, which become crowded together at the shell margin in fully grown forms, especially on the brachial valve; ventral interior with stout dental lamellae descending directly to the floor of the valve, extended as low ridges bounding an ovate muscle area; teeth blunt, with large and prominent crural fossettes lying close beneath them and rimmed by accessory teeth; dorsal interior with large cardinalia projecting above the hinge line, the width between the brachiophore tips being four-tenths the width of the valve; brachiophores blade-like, with massive knob-like ends, diverging at 90° and adpressed to the notothyrial platform; cardinal process a bulbous myophore without shaft, joined to the brachiophores at its posterior end; muscle scars extend to the longitudinal midline of the valve, the anterior pair the larger, not bilobed.

TYPE SPECIMENS (measurements in mm.)

		Length	Width
HOLOTYPE.	Internal and external moulds of brachial valve (BB.30525a–b)	5·2	—
PARATYPES.	Internal and external moulds of pedicle valve (BB.30526a–b) . . .	4·8	6·7
	Internal and external moulds of pedicle valve (BB.30527a–b) . . .	—	9·0 (est.)
	Internal and external moulds of brachial valve (BB.30528a–b) . . .	6·8	9·0 (est.)

TYPE HORIZON AND LOCALITY. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

DISCUSSION. The known species of *Panderina* were all erected by Pander and Lamansky (Schuchert & Cooper 1932 : 82), and form a homogeneous group of shells with characteristics 'intermediate between *Orthis s.s.* and *Productorthis*'. All have plano- or concave-convex shells, short interareas, simple cardinalia, and are imbricate anteriorly. The new species has imbricate growth lamellae, but they are not confined to the front of the shell. The brachial valve is also distinctly convex, though the specimens are distorted and the degree of convexity cannot be accurately measured. The cardinalia approach the *Productorthis* type, and are larger than in the other described species. It can be seen therefore that the new species has characters which place it a little further towards *Productorthis* than the other species of *Panderina*.

Family **DOLERORTHIDAE** Öpik 1934

Subfamily **DOLERORTHINAE** Öpik 1934

Genus ***DOLERORTHIS*** Schuchert & Cooper 1931

Dolerorthis cf. ***tenuicostata*** Williams 1955

(Pl. 4, figs. 4, 6–7)

FIGURED SPECIMEN (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30541a–b)	11·0	—

HORIZON AND LOCALITY. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

DISCUSSION. One specimen has been found, and shows the interarea and umbonal regions. Externally the ribs appear similar to those of *D. tenuicostata*, but since the specimen is not complete the patterns cannot be compared. Internally the muscle scars are of the same pattern, though the ridges bounding the diductor scars make an angle of 90° with each other while in the holotype of the species this angle is about 60°. The *vascula media* are typical of the genus. Since the brachial valve has not been found, and the full ribbing pattern cannot be analysed, the specific identification is not certain.

Subfamily **GLYPTORTHINAE** Schuchert & Cooper 1931

Genus ***PTYCHOPLEURELLA*** Schuchert & Cooper 1931

Ptychopleurella sp. (1)

(Pl. 3, figs. 19–23)

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30537a–b)	3·5	—
Internal and external moulds of brachial valve (BB.30538a–b)	4·5	—

Horizon and locality. Nantannog Formation, fine sandstones and shales south-east of Fferam-uchaf farm, Llanbabo. N.G.R. 36518657.

Discussion. The valves have the typical form of *Ptychopleurella*: the pedicle valve is sub-pyramidal, with a long, almost catacline interarea, the brachial valve is convex, with a median sulcus and a shorter, almost orthocline interarea, and both valves have typical interiors for the genus. The ornament is of simple, angular costae, fourteen on the brachial valve, with two in the sulcus, originating just anterior to the umbo. It is crossed by imbricate growth lamellae, crowded together in the first 5 mm. of growth, subsequently occurring at three per mm.

Only three pedicle valves and two brachial valves have been found, so that no good estimates of the size and shape parameters of the stock can be gained. The ratios of length to width as a percentage of the pedicle valve are 56·3, 58·8 and 79·7, and of the brachial valves 60·0 and 70·0. Without more material it is impossible to make any good comparisons with described species. In the simple ribs this species contrasts with *Ptychopleurella* sp. (2) from Llanbabo, and is similar to other early species, such as *P. oklahomensis* Cooper from the McLish formation, Llanvirn Series (Cooper 1956 : 388).

Ptychopleurella sp. (2)

(Pl. 4, figs. 1–3, 5)

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of incomplete brachial valve (BB. 30539a–b)	—	—
Internal and external moulds of incomplete pedicle valve (BB.30540a–b)	6·8	8·6 (est.)

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The valves found are small, biconvex and transverse, with a strongly convex pedicle valve with a median flattening and a strongly apsacline interarea, and a convex brachial valve with possibly a slight median fold and an almost orthocline interarea. The ornament is of coarse angular costae, increasing by implantation and crossed by close imbricate growth lamellae numbering eight per mm. at 6 mm. from the ventral umbo. Internally the dental lamellae are receding; the ventral musculature is well defined and elevated on a pseudospondylium, the adductor tracks being wide and shorter than the diductor tracks; the cardinalia are large, the cardinal process being a simple ridge somewhat thickened on its anterior edge.

The species is similar to the later species of *Ptychopleurella*, e.g. *P. bouchardi* (Davidson) from the middle Silurian, which have ribbing patterns characterized by late developing secondary costae. The slight median fold of the brachial valve, if found on other specimens, may prove to be a diagnostic feature, since it is not found in other species of the genus.

Family **PLAESIOMYIDAE** Schuchert 1913

Subfamily **PLAESIOMYINAE** Schuchert 1913

Genus ***PLAESIOMYS*** Hall & Clarke 1892

Plaesiomys cf. ***robusta*** (Bancroft)

(Pl. 4, figs. 8–12)

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30544a–b)	23·5	32·5
Internal and external moulds of pedicle valve (BB.30545a–b)	25·0	26·6 (est.)
Internal and external moulds of brachial valve (BB.30543a–b)	15·0	—

Horizon and locality. Crewyn Formation, grits in small outcrop 420 yds. west-south-west of Ysgubor-gader, Mynachdy. N.G.R. 29589214.

Discussion. Both valves have the typical characters of *Plaesiomys* in shape, ventral musculature, and cardinalia. The very poorly preserved external moulds have costellate ribbing. The pedicle adjustor scars are very distinct, the diductor scars slightly bilobed, and the adductor scars not differentiated. The length of the two pedicle valves varies from 70–90 per cent. of their width. Strong internal plications extend inwards from the margin. These features are listed by Bancroft (1945 : 244–245) as characteristic of *P. robusta*. He gives little idea of the natural variation within the species, and unfortunately does not figure a typical pedicle valve, but only one described by him as abnormal.

Plaesiomys (***Dinorthis***) sp.

(Pl. 4, figs. 13–15)

Figured specimen (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30542a–b)	8·0	10·0

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The valve is of a subquadrate *Dinorthis*, convex at the umbo, but becoming flat towards the commissure, the interarea short and apsacline, with an open delthyrium, and a simple costate ornament of eighteen costae, becoming broad and flat-topped towards the anterior. In the interior the muscle scars are subquadrate and slightly indented medianly, though the individual scars cannot be separated. The dental lamellae are widely divergent. The shape of the valve, and the number of costae suggest a young specimen of *D. flabellulum* (J. de C. Sowerby).

Family **PLECTORTHIDAE** Schuchert & Le Vene 1929

Subfamily **PLECTORTHINAE** Schuchert & Le Vene 1929

Genus ***PLECTORTHIS*** Hall & Clarke 1892

Plectorthis (?) sp.

(Pl. 4, figs. 16, 19)

1919 *Orthis* (*Dalmanella*) *testudinaria*? Dalman; Matley *in* Greenly : 452.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (Af.1377) . .	6·6	8·0
Internal mould of pedicle valve (Af.1462) . .	8·5	—

HORIZON AND LOCALITY. Nantannog Formation, gritty shales 250 yds. west-south-west of Fferam-uchaf, Llanbabo. N.G.R. 36178655.

DISCUSSION. The valves are convex, suboval in outline with a straight hinge-line narrower than the maximum width, and a short curved apsacline interarea and open delthyrium. The ornament is finely costellate. The teeth are not seen, the dental lamellae are thin and sub-parallel, the muscle scars extend one-third the length of the valve with the adductor and diductor scars the same length and with a rectangular end.

Subfamily **PLATYSTROPHIINAE** Schuchert & Le Vene 1929

Genus ***PLATYSTROPHIA*** King 1850

Platystrophia precedens major Williams 1955

(Pl. 4, figs. 17–18)

FIGURED SPECIMEN (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30546a–b)	13·5	—

HORIZON AND LOCALITY. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

DISCUSSION. Isolated valves referable to *Platystrophia* have been found at Careg-onen, Trwyn y Crewyn and Llanbabo. Only at the last locality are the valves complete enough for a specific identification, and appear to be identical with specimens from the Derfel Limestone (Whittington & Williams 1955 : 402, pl. 38, figs. 24–29). The other specimens, in all probabliity from the same horizon, also belong to the bicostate species group.

Family **SKENIDIIDAE** Kozlowski 1929

Genus ***SKENIDIOIDES*** Schuchert & Cooper 1931

Skenidioides sp. (1)

(Pl. 5, figs. 1–2)

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30547) . .	2·3	3·0
Internal mould of brachial valve (BB.30548) .	3·2	—

Horizon and locality. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

Discussion. The specimens are preserved as internal and external moulds in a coarse grit, and are too poorly preserved to identify specifically. In particular the costae are hardly preserved at all, though they are probably few in number, between 13 and 16, and simple. The pedicle valve is semicircular, pyramidal, with a long strongly apsacline interarea and a high-standing shallow spondylium supported by a short receding median septum. The brachial valve is gently convex and sulcate, and bears a well developed median septum running the length of the valve.

Table 3

$\bar{l}$ mm. (var. l)	2·47 (0·203)
$\bar{w}$ mm. (var. w)	3·53 (0·306)
r	0·723
a (var. a)	1·245 (0·0493)
b (var. b)	0·45 (0·3126)

Table 3. Statistics of length (l) and width (w) of fifteen pedicle valves of *Skenidioides* sp. (1).

Skenidioides sp. (2)

(Pl. 5, figs. 3–5)

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of brachial valve (BB.30549a–b)	2·3	—
Internal and external moulds of pedicle valve (BB.30550a–b)	2·6	—

Horizon and locality. Nantannog Formation, fine sandstones and shales 190 yds. south-east of Fferam-uchaf, Llanbabo. N.G.R. 36518657.

Discussion. The specimens are typical of the genus, but are very small. The pedicle valve is sub-pyramidal, with a shallow, largely free spondylium. The brachial valve has a good septalium, the supporting plates converging on a high median septum which runs most of the length of the valve. The ornament of both valves is of simple costae, apparently about fourteen in number.

This species is very similar to *Skenidioides* sp. (1) from the *D. hirundo* zone, but there seem to be minor differences between the interiors of the two species. The earlier species has a well developed median septum in the pedicle valve, possibly with a larger delthyrium. The dorsal sulcus also seems to be better developed in this species.

Superfamily **ENTELETACEA** Waagen 1884

Family **PAURORTHIDAE** Öpik 1933

Genus ***PAURORTHIS*** Schuchert & Cooper 1931

Paurorthis (?) sp.

(Pl. 5, figs. 6–9)

Description. Pedicle valve subcircular, evenly convex, about one-third as deep as long and slightly longer than wide; hingeline slightly less than the maximum width; interarea curved, apsacline, delthyrium open; ornament fascicostellate but not well preserved; umbonal cavity deep; muscle scars extending forwards beyond the umbonal cavity to almost half the length of the valve, elevated anteriorly; central (adductor?) scars occupying most of the width between the dental lamellae, flanked by narrow, slightly depressed (diductor?) tracks which extend onto the sides of the dental lamellae, which extend alongside them as ridges; teeth apparently aligned along the dental lamellae, crural fossettes present; vascula media at first converging from the ends of the diductor scars, then diverging; margin of valve crenulate.

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30603a) .	9·5	10·2
Internal and external mould of pedicle valve (BB.30604a–b)	10·3	9·4

Horizon and locality. Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach Cottage, Bod Deiniol. N.G.R. 37688528.

Discussion. Although a number of pedicle valves were collected, no brachial valves were found, nor was it possible to examine a thin section of the shell to determine the nature of the shell material. The fascicostellate ornament, disposition of the muscle scars and vascula media, and the short median ridge are all found in *Paurorthis*. Williams (1962 : 141) has commented on the development of the latter feature, which is better developed in the allied genus, *Cyclomyonia*.

The valves also show some similarities to certain dalmanellid-like members of the Orthidae and Finkelnburgiidae. Pedicle valves of *Nanorthis* have a similar shape, with sometimes a fasciculate ornament, but internally the shell is not thickened under the muscle scars; *Nothorthis* is similar but more transverse. *Archaeorthis* also has a *Dalmanella*-like exterior, but the muscle scars, although elevated, do not extend forwards from the umbonal cavity as in the Anglesey specimens. *Diparelasma* is another dalmanellid-like form, with the muscle scars elevated in a pseudospondylium in front, and a short median ridge, but with a finely costellate ornament. In many respects the muscle scars and pseudospondylium are very similar.

Family **DALMANELLIDAE** Schuchert 1913

Genus ***DALMANELLA*** Hall & Clarke 1892

Dalmanella (?) sp.

(Pl. 5, figs. 10–11)

Figured specimens (measurements in mm.)

	Length	Width
External mould of brachial valve (BB.30568) .	8.2 (est)	—
External mould of pedicle valve (BB.30569) . .	7·2	8·4 (est.)

Horizon and locality. Crewyn Formation, grits 420 yds. west-south-west of Ysgubor-gader. N.G.R. 29589214.

Discussion. The valves are small, and the interiors are very badly preserved, so that it is impossible to make out the details of the cardinalia in the brachial valve. Owing to the small size of the brachial valve the ribbing pattern is not fully developed, so that only the first internal and external branches are developed. The pedicle valve is deeply convex, and only slightly carinate, the brachial valve very gently convex with a shallow median sulcus.

Genus ***ONNIELLA*** Bancroft 1928

Onniella (?) sp.

(Pl. 5, figs. 12–14)

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30570a–b)	—	8·1
Internal mould of brachial valve (BB.30571) .	5·5	6·4

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The valves are subcircular, biconvex, the pedicle valve having the greater convexity and the brachial valve a shallow sulcus. The ornament is only seen on the pedicle valve and is slightly fascicostellate with forty to fifty costellae on the margin and a wavelength of 0·23 mm. at 5 mm. from the ventral umbo. The ventral adductor scar is shorter than, but not enclosed by the diductor scars, from the ends of which run widely separated and diverging *vascula media*. The brachiophores are widely divergent, but the details of the fulcral and supporting plates are not seen. The former may not be present. The adductor scars in the brachial valve are quadripartite. The valves recall *Onniella* (*Soudleyella*) cf. *avelinei* Bancroft (Whittington & Williams 1955 : 407).

Family **HARKNESSELLIDAE** Bancroft 1928

Genus ***HARKNESSELLA*** Reed 1917

Harknessella (?) sp.

(Pl. 5, fig. 16)

Figured specimen (measurements in mm.)

	Length	Width
Exterior of pedicle valve (Af.1492)	10·1	14·7

Horizon and locality. Garn Formation, limestone block in breccia bed, 300 yds. south-east of the summit of Mynydd-y-garn. N.G.R. 31759062.

Discussion. The valve is convex and slightly carinate, with a costellate ornament, no other details can be seen. A carinate pedicle valve is a feature of *Harknessella.*

Genus ***HORDERLEYELLA*** Bancroft 1928

Horderleyella (?) sp.

(Pl. 5, fig. 15)

Figured specimen. Incomplete internal mould of pedicle valve (BB.30572).

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. An internal mould of a pedicle valve from Llanbabo agrees with *Horderleyella*? sp. from the Derfel Limestone (Whittington & Williams 1955, pl. 38, fig. 30) in having similar small subcordate muscle scars, and possibly belonging to an undescribed species.

Family **LINOPORELLIDAE** Schuchert & Cooper 1931

Genus ***SALOPIA*** Williams 1955

Salopia salteri gracilis Williams

(Pl. 5, figs. 17–18)

Figured specimen. Incomplete internal mould of brachial valve (BB.30573.)

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The cardinalia and the median septum are well preserved, and show that the specimens belong to the genus *Salopia.* Since the cardinalia are small, with a length of less than 20 per cent. of the valve length, it can be placed in the subspecies *S. salteri gracilis.*

Family **ANGUSTICARDINIIDAE** Schuchert & Cooper 1931

Genus ***RHYNCHORTHIS*** nov.

DIAGNOSIS. Rostrate biconvex shells, the brachial valve with the greater convexity; rectimarginate or slightly uniplicate; hinge-line narrow; ventral interarea long and narrow, almost orthocline, delthyrium open; dorsal interarea shorter, almost orthocline, notothyrium open; ornament on both valves of simple rounded costae becoming vague towards the flanks.

Ventral interior with receding, almost obsolete dental lamellae; strong teeth, oval in shape and aligned along the lamellae; orthoid muscle scars, the adductor and diductor scars expanding forwards, the former not enclosed by the latter.

Dorsal interior with deep notothyrial cavity, cardinal process a simple ridge; brachiophores plate-like, short and thick, with supporting and socket plates; adductor muscle scars orthoid, differentiated into anterior and posterior pairs, the anterior pair the larger.

TYPE SPECIES. *Rhynchorthis rotundus* sp. nov. from the Treiorwerth Formation.

DISCUSSION. Schuchert & Cooper (1931 : 244) erected the subfamily *Angusticardiniinae*, with their new genus *Angusticardinia*, for orthids evolving towards the rhynchonellids, but still retaining more orthid characters than those of the rhynchonellids. *Rhynchorthis* conforms to the description of the subfamily in having interareas on both valves, together with both orthid and rhynchonellid characters. It differs, however, from *Angusticardinia* in a number of important features. The interareas, though narrow, are long, the dental lamellae are weak or obsolete, and there is no median ridge inside the brachial valve. It is not known whether the shell material of either genus is punctate; Öpik (1933 : 5, 6) thought that *Angusticardinia* was probably punctate.

Apatorthis (Öpik 1933 : 5, from the middle and upper Ordovician of Estonia) is another rhynchonelliform shell, but has short and narrow curved interareas of equal length, a well marked fold and sulcus, and angular costae. The shell is punctate and is placed by Öpik in the *Enteletacea*.

Schuchert & Cooper (1932 : 84) suggested that *Angusticardinia*, being 'the earliest rhynchonelliform shell known', may have been the ancestor of the rhynchonellids, evolving into *Rhynchotrema*. *Rhynchorthis* is contemporary with *Angusticardinia*, but seems to be closer in structure to the ancestral orthids. The hinge-line is not quite so narrow, the interareas are long, and the cruralium-like structure of *Angusticardinia*, in which the supporting plates meet a median ridge, is not developed.

Rhynchorthis rotundus gen. et sp. nov.

(Pl. 5, figs. 19–26)

DIAGNOSIS. Species of *Rhynchorthis*, six-fifths as long as wide, dorsi-biconvex with brachial valve one-fifth as deep as long, pedicle valve one-eighth as deep as long, ornamented by about twelve simple costae; internal details as for genus.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	Internal mould of brachial valve (BB. 30551)	10·1	8·4
Paratypes.	Internal mould of brachial valve (BB. 30552)	11·1	—
	Internal mould of brachial valve (BB. 30553)	—	—
	Internal mould of pedicle valve (BB. 30554)	—	—
	Internal mould of pedicle valve (BB. 30556)	12·4	9·5

Type horizon and locality. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

Discussion. The new species is known from a number of rather poorly preserved moulds, particularly so in the case of the external moulds. The mean length per cent. of 5 pedicle valves relative to the width is 121·0 (variance 195·0). The corresponding figures for 5 brachial valves are 107·4 and 121·5. In the five brachial valves the mean depth per cent. relative to length is 20·6 (variance 29·2).

Suborder CLITAMBONITIDINA Öpik 1934

Superfamily **CLITAMBONITACEA** Winchell & Schuchert 1893

Family **POLYTOECHIIDAE** Öpik 1934

Genus ***TRITOECHIA*** Ulrich & Cooper 1936

Tritoechia sp.

(Pl. 6, figs. 1–3, 5)

Figured specimen (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30557a–b)	17·0	19·8 (est.)

Horizon and locality. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

Discussion. Only one well preserved pedicle valve, the figured specimen, and a few other poorly preserved pedicle valves have been found. No brachial valves have been found which can definitely be assigned to the genus.

The valve conforms externally to the genus *Tritoechia*. In outline it is semicircular, widest at the hinge-line, with cardinal angles just acute. The surface is evenly convex, the umbo not incurved or inflated, and the interarea plane, apsacline but almost catacline. The delthyrium is covered by a strongly convex deltidium, but the foramen is not preserved. The ornament, which is poorly preserved, is finely multicostellate, with about fourteen costellae in 5 mm. both at the margin and near the umbo. Internally the teeth are strong and rounded, supported by receding dental lamellae which diverge ventrally. The form and extent of the muscle scars are not known.

Among the species of *Tritoechia* described by Ulrich & Cooper (1938 : 162–169) are a number which approach the valve closely, the nearest being *T. transversa*, which has an interarea more inclined towards the orthocline.

Family **CLITAMBONITIDAE** Winchell & Schuchert 1893

Subfamily **CLITAMBONITINAE** Winchell & Schuchert 1893

Genus ***CLITAMBONITES*** Pander 1830

Clitambonites (?) sp.

(Pl. 6, fig. 4)

Figured specimen. Fragmentary external mould of brachial valve (BB.30558).

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The external mould is of a large, probably subquadrate brachial valve in excess of 18 mm. long by 26 mm. wide, gently convex, becoming flat or slightly sulcate medianly. The ornament is mulitcostellate, with perhaps four costellae per cm. at 5 mm. from the umbo, and at the margin eighteen per cm. At least ten more prominent ribs divide the ornament into sectors, each with four to six smaller ribs, arising both by implantation and bifurcation. Strong thick growth lamellae occur at intervals. The convex shape, and prominent growth lamellae, are both features of *Clitambonites*. *Clinambon* and *Vellamo* both have much less prominent growth costellae.

Genus ***ILMARINIA*** Öpik 1934

Ilmarinia sp.

(Pl. 6, figs. 6–7)

Figured specimen. Internal and external moulds of incomplete pedicle valve (BB.30559a–b).

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. Two counterpart moulds of the pedicle valve of a clitambonitaceid from Llanbabo show a subquadrate outline, a long apsacline interarea, and a slight sulcus. The delthyrium is possibly open, or constricted by deltidial plates, because there are certainly traces of a large foramen, and the ornament is finely multicostellate. Internally there is a good spondylium, one-third the width of the valve, and elevated by its own depth from the floor of the valve. It has a flat floor, and (though the specimen is broken) shows what may be the beginning of a thin receding median septum. *Ilmarinia* is the only clitambonitaceid genus with a ventral sulcus, and hence the specimen probably belongs here.

Subfamily **ATELELASMATINAE** Cooper 1956

Genus ***APOMATELLA*** Schuchert & Cooper 1931

Apomatella (?) sp.

(Pl. 6, figs. 8–11)

Description. Pedicle valve subquadrate, wider than long, widest at the hinge-line with the cardinal angles right angles; deeply pyramidal, slightly flattened medianly, interarea catacline or strongly apsacline, slightly curved, twice as wide as long; delthyrium probably open; ornament finely costellate; spondylium simplex high, shallow in cross-section; median septum receding.

Figured specimens (measurement in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30605a–b)	—	8·8
Internal and external moulds of pedicle valve (BB.30606a–b)	10·9	13·4 (est.)

Horizon and locality. Bod Deiniol Formation, Grits in temporary excavation 50 yds. north of Ty-bach Cottage, Bod Deiniol. N.G.R. 37688528.

Discussion. A number of pedicle valves have been found at this locality, none with any trace of plates restricting the delthyrium, suggesting that the absence of plates is more than an accident of preservation.

Superfamily **GONAMBONITACEA** Schuchert & Cooper 1931

Family **GONAMBONITIDAE** Schuchert & Cooper 1931

Subfamily **GONAMBONITINAE** Schuchert & Cooper 1931

Genus ***ANTIGONAMBONITES*** Öpik 1934

Antigonambonites pyramidalis sp. nov.

(Pl. 6, figs. 12–18)

Diagnosis. Outline sub-rectangular, wider than long, hinge-line just less than maximum width, anterior and lateral commissures rectimarginate; biconvex, pedicle valve pyramidal, with a long almost catacline interarea, slightly curved, brachial valve slightly convex, with a shallow median sulcus, interarea short and anacline; delthyrium probably closed or restricted by convex deltidial plates; notothyrium restricted but not closed by chilidial plates; ornament costellate, costellae numbering four per mm. at 5 mm. from the umbo, stronger ribs appearing at intervals, ribs crossed by well marked growth lines giving a slightly imbricate appearance; teeth not seen in ventral interior, but muscle scars impressed on a largely sessile *spondylium triplex*, supported at its anterior end by two lateral septa, the median septum being almost obsolete, adductor and diductor scars expanding forwards, the adductor tracks separated from the diductor tracks by raised ridges; dorsal interior with brachiophores long and widely divergent, measuring between their tips over half the width of the valve, median septum very short or absent, cardinal process simple; adductor muscle scars within a semicircular track bounded by the brachiophores and by an indented ridge; margin crenulated.

TYPE SPECIMENS (measurements in mm.)

		Length	Width
HOLOTYPE.	Internal and external moulds of brachial valve (BB.30561a–b)	5·8	7·5
PARATYPES.	Internal mould of pedicle valve (BB. 30562)	—	—
	Internal mould of brachial valve (B.30563)	9·9	—
	Internal mould of pedicle valve (BB. 30564)	6·8	—

TYPE HORIZON AND LOCALITY. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

DISCUSSION. The poor preservation of the specimens, and the fact that they are preserved as natural moulds and not as complete specimens with the original shell material, means that it is impossible to study the form and structure of the spondylium in detail. Since, however, it is a *spondylium triplex* the specimens belong to the Gonambonitidae. *Antigonambonites* Öpik is the closest described genus, being biconvex and having a largely sessile spondylium. The described species are generally flatly lenticular, with an apsacline interarea in the pedicle valve. The ornament is similar to that of *A. costatus* Öpik (1934 : 156), in which the costellae are conspicuous and angular, though in this species some costellae are accentuated. The pedicle valve is also deeper, in shape like that of *Skenidioides*, and has a similarly inclined interarea. The deltidial plates are poorly preserved in the moulds, and it is impossible to say whether they meet medianly or not. The mean percentage length relative to width of 5 brachial valves is 76·0, with a range from 58·2 to 92·9.

Genus *ESTLANDIA* Schuchert & Cooper 1931

Estlandia (?) sp.

(Pl. 7, figs. 2–4, 6–9)

1919 *Petraia* sp. Greenly : 435.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal and external moulds of incomplete pedicle valve (Af.238, Af.225)	—	—
Internal mould of brachial valve (Af.214) . . .	5·4	—
Internal and external moulds of brachial valve (BB.30560a–b)	distorted	

HORIZON AND LOCALITY. Berw-uchaf Grits, 90 yds. north of Bwlch-gwyn farm, Holland Arms. N.G.R. 48207303.

Discussion. The pedicle valve is strongly pyramidal, with a long apsacline interarea, possibly with an open delthyrium and with a costellate surface, the costellae having the 'chain-sculpture' characteristic of *Estlandia*. The interior has a well developed *spondylium triplex*, with a thick median septum, and thinner lateral septa parallel to the median septum. The interior of the brachial valve has long widely divergent brachiophores, thickened at their outer ends. The adductor muscle scars are half the length of the valve, pentagonal in form, with crenulated antero-lateral margins. They are separated by a thin median septum which joins the brachiophores at their inner ends to form an anchor-shaped structure.

The valves are provisionally placed in *Estlandia* as the ornament of the pedicle valve is quite characteristic of that genus. The side septa of *Estlandia*, however, are usually short and widely spaced, rather than close to the median septum.

Family **KULLERVOIDAE** Öpik 1934

Genus ***KULLERVO*** Öpik 1932

Kullervo aff. ***panderi*** (Öpik)

(Pl. 6, figs. 19–22; Pl. 7, fig. 1)

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30565) . .	distorted	
Internal mould of pedicle valve (BB.30566) . .	3·3	7·5
Internal and external moulds of brachial valve (BB.30567a–b)	4·5	8·5

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The specimens are certainly conspecific with *Kullervo* aff. *panderi* (Öpik) described by Williams (Whittington & Williams 1955 : 412, pl. 30, figs. 56–62) and, like it, differ from Öpik's species only in the poorer development of the hemi-syrinx. The cardinal angles are slightly alate, and on them the concentric ornament is more pronounced than medianly (cf. Öpik 1934 text-fig. 37). The ventral interarea is almost catacline and appears to have an open delthyrium; since the specimens are small this is probably a characteristic of young stages, as suggested by Williams (Whittington & Williams 1955 : 412). There are no sub-spondylial septa.

Suborder CLITAMBONITIDINA Öpik 1934

Superfamily and genus uncertain

(Pl. 7, figs. 5, 10–11)

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30607) . .	—	—
Internal and external moulds of brachial valve (BB.30608a–b)	8·0	14·6

Horizon and locality. Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach Cottage, Bod Deiniol. N.G.R. 37688528.

Discussion. Two valves found in the Nantannog Beds at the site of the Alaw reservoir cannot be assigned to any clitambonitid species. In particular it is not certain whether they belong together. The pedicle valve has a very long interarea, with deltidial plates, dental lamellae which converge to the floor of the valve, possibly with side septa, and with a prominent central groove in the floor of the delthyrium; the ornament is coarsely costellate. If the structure is a spondylium simplex then the valve may belong to the Polytoechiidae, as the median septum seems only to be rudimentary. The brachial valve is quadrate in outline, slightly alate, convex with a shallow median sulcus, and a short, almost orthocline interarea, possibly with a small chilidium; the ornament is coarsely costellate and imbricate. Internally the cardinalia are elevated on a notothyrial platform, which passes into a broad median septum; the cardinal process is a simple ridge, with widely divergent socket ridges; the muscle scars have two pairs of septa lying lateral to them, parallel to the median septum.

Order STROPHOMENIDA Öpik 1934

Suborder STROPHOMENIDINA Öpik 1934

Superfamily **PLECTAMBONITACEA** Jones 1928

Family **PLECTAMBONITIDAE** Jones 1928

Subfamily **AHTIELLINAE** Öpik 1933

Genus ***AHTIELLA*** Öpik 1932

Ahtiella quadrata sp. nov.

(Pl. 8, figs. 1–9)

Diagnosis. Alate, subrectangular *Ahtiella*, two-thirds as long as wide; brachial valve convex, with a median sulcus widening and deepening anteriorly, flanked by rounded folds and slightly concave flanks near the cardinal angles; anterior commissure bent ventrally in some specimens; interarea anacline, notothyrium possibly covered by a small convex chilidium at its apex; pedicle valve flat or concave, with a low carinate median fold, and the anterior and lateral commissures bent ventrally; delthyrium open, possibly covered by a small arched plate at its apex; interarea strongly apsacline, eight times as wide as long; ornament of about fifteen costellae in 5 mm. at 5 mm. from the ventral umbo, every third or fourth costella accentuated, pedicle valve with about three very oblique and indistinct wrinkles near the cardinal angles; teeth angular, aligned along the hingeline, supported by very short receding dental lamellae diverging to the floor of the valve; muscle scars rectangular, wider than long, adductor scars not enclosed by diductor scars, both pairs expanding linearly forwards, adductors enclosing an angle of 60° with an arcuate anterior margin, diductors blade-like, extending beyond the adductors, enclosing an angle of 75° between their outer margins; small depressions beneath teeth are either pedicle adjustor scars or depressions to accommodate the socket ridges; two pairs of vague ridges radiate from the ends of the diductor scars; anterior and lateral margins abruptly deflected ventrally; cardinalia orthid, elevated on a notothyrial platform; cardinal process a simple ridge, thickened along its anterior edge, highest midway along its length and triangular in outline; socket ridges short and rod-like, diverging at about 90°, resting directly on the notothyrial platform and possibly continuous with an incipient chilidium; sockets broad excavations in the hinge-line, diverging at about 90° and each enclosing an angle of 20°; prominent median septum separating the muscle scars, which are disposed in an arc about the umbo, extending just less than half the length of the valve, one pair lateral to the other.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	Internal mould of pedicle valve (BB.30609)	10·9	15·8
Paratypes.	Internal mould of pedicle valve (BB. 30610)	13·3	21·2 (est.)
	Internal and external moulds of pedicle valve (BB.30611a–b) . . .	—	22·0 (est.)
	Internal and external moulds of brachial valve (BB.30612a–b) . . .	—	—
	Internal and external moulds of brachial valve (BB.30613a–b) . . .	—	—
	Internal and external moulds of brachial valve (BB.30614a–b) . . .	—	—

Type horizon and locality. Torllwyn Formation, sandstones 50 ft. above the base of the succession on the north side of the faulted syncline, 45 yds. north of Ogof Gynfor, Llanbadrig. N.G.R. 37859490.

Ahtiella concava sp. nov.

(Pl. 7, figs. 12–22)

Diagnosis. Semicircular slightly alate *Ahtiella*, six-tenths as wide as long; brachial valve evenly convex in lateral view, with a narrow median sulcus having a V-shaped cross-section, flanked by rounded folds; interarea anacline to almost orthocline, very short, notothyrium possibly covered by a small convex chilidium at its apex; pedicle valve convex in lateral view, becoming more strongly bent towards the anterior commissure, but with the convexity broken by a narrow carinate fold which becomes more rounded and vaguer away from the umbo; delthyrium covered by a small arched plate at its apex; interarea procline or catacline, one-thirteenth as long as wide; ornament on both valves too fine to be observed, but growth lines present near the margins of valves; teeth triangular, aligned along the hinge-line, supported by very short receding dental lamellae diverging to the floor of the valve; muscle scars rectangular, diductors extending further forwards than adductors, but details not seen; vague ridges radiating from the diductor scars; anterior and lateral margins deflected ventrally in some specimens; dorsal cardinalia orthid, elevated on a notothyrial platform; cardinal process a simple ridge, triangular in side view and thickened along its anterior margin; socket ridges short and rod-like, diverging at 90°, sockets shallow excavations under the hinge-line; muscle scars separated by a prominent median septum, posterior scars rounded and set in excavations under the notothyrial platform, anterior scars elongate and lying along each side of the median septum, extending to almost half the length of the valve, flanked by three ridges on each side, radiating from the posterior scars; median septum cusp-shaped in lateral outline, highest at its mid-point, thickened and swollen in its anterior half.

TYPE SPECIMENS (measurements in mm.)

		Length	Width
HOLOTYPE.	Internal and external moulds of pedicle valve (BB.30615a–b) . . .	17·2	23·8
		(distorted)	
PARATYPES.	Internal and external moulds of brachial valve (BB.30616a–b) . . .	—	19·8
		(distorted)	
	Internal and external moulds of brachial valve (BB.30617a–b) . . .	—	—
	Internal and external moulds of brachial valve (BB.30618a-b) . . .	13·0	20·7 (est.)
	Internal and external moulds of pedicle valve (BB.30619a–b) . . .	11·7	22·2
		(distorted)	

TYPE HORIZON AND LOCALITY. Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach Cottage, Bod Deiniol. N.G.R. 37688528.

DISCUSSION. The two Anglesey species of *Ahtiella* differ from each other mainly in external shape and ornament, and in the development of the internal ridges in the brachial valve. *A. quadrata* has a rectangular outline, with the pedicle valve almost flat across the visceral disc and the brachial valve gently convex; both fold and sulcus are shallow. The ventral interarea is apsacline, and the ornament unequally costellate. In contrast *A. concava* is semicircular in outline, the pedicle valve has a concave visceral disc, and the brachial valve is strongly convex; both fold and sulcus are carinate, and higher and deeper. The ventral interarea is procline to catacline, and the ornament, though not preserved, is probably much finer.

Both species differ in their combinations of characters from the Baltic species described by Öpik (1932; 1933) and Hessland (1949). Most of these are relatively much wider, with prominent rugae close to the hinge-line. The fold and sulcus of *A. concava* are much better developed than in any Baltic species, although in outline and convexity it is similar to *A. lirata* Öpik. *A. quadrata* is more quadrate than any of the Baltic forms, and less convex.

The mean percentage of length relative to width of five pedicle valves of *A. quadrata* was 64·7 (range 57·3–69·0). For *A. concava* the corresponding value for thirteen pedicle valves was 59·8 (range 51·7–77·0) and for eight brachial valves 62·1 (range 54·9–78·4). Correlation coefficients between length and width for these specimens were not significant, due to poor preservation and distortion of the specimens. For similar reasons it was not possible to make any accurate estimate of the thickness of the valves.

Genus ***REINVERSELLA*** nov.

DIAGNOSIS. Semicircular plectambonitaceans with small postolateral wings; abruptly geniculate, with the border deflected ventrally; ventral disc convex, dorsal disc flat, the anterior and lateral commissures with a frill or gutter deflected dorsally; ventral interarea apsacline, short and wide, dorsal interarea short, anacline, both delthyrium and notothyrium open; ornament of fine bifurcating costellae, crossed by irregular concentric rugae on the visceral disc.

Ventral interior with dental lamellae diverging widely both laterally and ventrally, continuous with low ridges round the muscle scars; muscle scars triangular, adductor and diductor scars equal in length.

Dorsal interior with cardinalia raised on a low notothyrial platform; cardinal process low, thin and blade-like, slightly swollen anteriorly; brachiophores short and triangular in section, continuous on their ventral faces with the interarea.

TYPE SPECIES. *Reinversella monensis* sp. nov. from the Treiorwerth Formation.

DISCUSSION. This genus is separated from *Inversella* Öpik because of the development of a second deflection of the anterior and lateral borders of the shell, which forms a sort of frill or gutter. A similar, but more elaborate frill is characteristic of *Limbimurina* Cooper (1956 : 851–852), which bears the same relationship to the strophomenacean *Leptaena* as the new genus does to *Inversella*. Two of the described species of *Inversella*, *I. borealis* Öpik and *I. angulata* Öpik, have a chilidium, and it may be present in the third species *I. perundosa* Öpik. In contrast the new genus has an open notothyrium.

Reinversella monensis gen. et sp. nov.

(Pl. 8, figs. 10–17)

1919 *Leptaena rhomboidalis* (Wilckens), *partim.*; Matley *in* Greenly : 442.

DIAGNOSIS. A species of *Reinversella* three-quarters as wide as long, and about one-third as deep as wide, ornamented with fine bifurcating costellae numbering fourteen to seventeen per 5 mm. on the rim of the visceral disc, crossed by seven to nine rugae, continuous or anastomosing across the midline; in the ventral interior the width of the muscle scars is about one-fifth the width of the valve and their length one-quarter the length of the valve; the width of the cardinalia is one-fifth the width of the brachial valve.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	External and internal moulds of brachial valve (BB.30574a–b)	15·3	21·3
		(distorted)	
Paratypes.	External and internal moulds of pedicle valve (BB.30575a–b) . . .	—	—
	External and internal moulds of brachial valve (BB.30576a—b) . . .	15·5	18·0 (est.)

Type horizon and locality. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

Discussion. In addition to bearing a frill, the new species shows detail differences from the described species of *Inversella*. *I. perundosa* Öpik from the Expansus-schiefer, *D. hirundo* zone (Öpik 1939 : 128, 142, Pl. 5, fig. 6) is the closest species, but has a prominent broad median costella.

Family **LEPTESTIIDAE** Öpik 1933

Subfamily **LEPTESTIINAE** Öpik 1933

Genus ***PALAEOSTROPHOMENA*** Holtedahl 1916

Palaeostrophomena sp.

(Pl. 9, figs. 2, 4–5)

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30579a–b)	7·6	—
Internal mould of brachial valve (BB.30580) . .	—	—

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The pedicle valve is subquadrate, and gently convex. The ornament consists of fine costellae, divided into sectors each containing five to seven costellae separated by stronger costellae numbering about thirty. Internally there appear to be no dental lamellae, other details have been obliterated. The brachial valve shows the cardinalia, the cardinal process is a rounded mass (as preserved) passing into a median septum, the sockets and accessory sockets are conspicuous. The specimens agree in all visible details with *P. magnifica* Williams, but the form of the ventral muscle scars, one of the diagnostic features of that species, is not visible in the Llanbabo specimens.

Palaeostrophomena (?) sp.

(Pl. 9, fig. 1)

FIGURED SPECIMEN (measurements in mm.)

	Length	Width
Exterior of pedicle(?) valve (BB.30581a–b) . .	11·7	24·0 (est.)

HORIZON AND LOCALITY. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

DISCUSSION. The valve is semicircular and gently convex. The posterior margin forms a slight angle at the umbo, the cardinal angles are acute, produced into small wings, and the lateral and anterior margins evenly curved. The ornament is of fine parvicostellae, separated into sectors containing sixteen in each by sharp accentuated costellae, about twelve in number in the whole valve, all the costellae arising by implantation. The surface of the valve is wrinkled along the posterior margin by radial rugae, which are more faintly developed over the whole surface.

The valve cannot be closely compared with *Palaeostrophomena* sp., as the interior is not exposed, but it agrees with the genus in exterior details. The closest species is *P. magnifica* Williams, though the number of parvicostellae in each sector is different. It could also belong to *Glyptambonites* Cooper, in which the pedicle valve has the same outline, convexity and ornament.

Family **LEPTELLINIDAE** Ulrich & Cooper 1936

Subfamily **LEPTESTIININAE** Havlíček 1961

Genus ***LEPTESTIINA*** Havlíček 1952

Leptestiina derfelensis (Jones)

(Pl. 9, figs. 7–9)

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30577) . .	4·8	—
Internal mould of brachial valve (BB.30578) .	—	—

HORIZON AND LOCALITY. Tandinas Shales, by the track 50 yds. west of Tandinas quarry, Careg-onen. N.G.R. 58248187.

DISCUSSION. Both valves show the internal characters well, particularly the brachial valve, in which the cardinalia and the lophophore platform are perfectly preserved. The papillae are not visible in the pedicle valve.

Genus ***BILOBIA*** Cooper 1956

Bilobia aff. ***musca*** (Öpik 1930)

(Pl. 9, figs. 10–13)

DESCRIPTION. Triangular *Bilobia* with rounded cardinal angles and an anterior tongue, four-fifths as long as wide; the brachial valve evenly concave and the pedicle valve slightly carinate with flattened flanks; teeth double, the posterolateral pair the larger; dental lamellae divergent, continuous with a raised rim to the muscle scars which is indented medianly in a right angle; diductor scars large and flabellate with small auxiliary lobes under the teeth, possibly just meeting anterior to the adductor scars and extending one-third the length of the valve; *vascula media* converging anteriorly from the ends of the diductor scars; dorsal lophophore platform prominent, one-half the length of the valve, elevated and free anteriorly, markedly bilobed with each lobe rounded.

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30582) . .	10·3	10·6
Internal mould of brachial valve (BB.30583) . .	—	—

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, 180 yds. east of Fferam-uchaf, Llanbabo. N.G.R. 36548673.

Discussion. The pedicle valve is very similar to that of *Bilobia musca* (Öpik) in the general shape, the form of the teeth, and the muscle scars. In the brachial valve the lophophore platform has similar rounded anterior lobes. None of the specimens shows the cardinalia, and there are no external moulds well enough preserved to show the ornament.

Family **SOWERBYELLIDAE** Öpik 1930

Subfamily **SOWERBYELLINAE** Öpik 1930

Genus ***EOPLECTODONTA*** Kozlowski 1929

Eoplectodonta lenis Williams

(Pl. 9, figs. 14–18)

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30584a–b)	—	—
Internal and external moulds of brachial valve (BB.30585a–b)	5·7	—
External mould of brachial valve with interarea of pedicle valve (BB.30586)	—	—

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo. N.G.R. 37758672.

Discussion. The interior of the pedicle valve conforms to that of *E. lenis* from the Derfel Limestone, though the denticles are only poorly seen on the right side. The dorsal muscle scars are raised on low platforms, and are flabellate in form with one pair outside the other. The median and submedian septa are almost parallel, and between the scars are distinct depressions running their full length.

Subfamily **PTYCHOGLYPTINAE** Cooper 1956

Genus ***PTYCHOGLYPTUS*** Willard 1928

Ptychoglyptus sp.

(Pl. 10, figs. 1–2)

Description. Pedicle valve semicircular, slightly alate, gently convex; brachial valve concave medianly with flattened wings; ornament divided into sectors by sharp accentuated costae and costellae, 8 at the margin of valve 4 mm. long, possibly three primary, the others arising about 1·5 mm. from the umbo; between are fine parvicostellae, too poorly preserved to be counted; concentric ornament of prominent rugae, faint at less than 2mm. from the umbo, slightly asymmetrical in cross section, steeper towards the umbo; divided into sectors by the sharp costellae which they do not cross or fold, in the median part of the valves alternating between them, laterally tending to coincide across them, bent convex to the umbo; fine concentric growth lines follow the rugae, hence the valve margin is scalloped.

Figured specimens (measurements in mm.)

	Length	Width
Exterior of pedicle valve (BB.30590) . . .	4·4	—
Exterior of brachial valve (BB.30589) . . .	—	—

Horizon and locality. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The valves are all small, none being above 5 mm. long; since most described members of the genus are up to four times this length it is possible that these are all young specimens, not affording adequate material upon which to erect a new species. *Ptychoglyptus kindlei* Cooper (1956 : 816) appears similar, but grows to a much larger size and develops a geniculation. *P. virginiensis* Willard (Cooper 1956 : 818) is also similar though the rugae seem to become prominent at an earlier growth stage. *P. valdari* (Spjeldnaes 1957 : 58; Williams 1962 : 194) has rugae with both faces sloping anteriorly, with the posterior face undercut, and this is also true of *P.* cf. *valdari* from Girvan (Williams 1962 : 194). *P.* cf. *virginiensis*, also from Girvan (Williams 1962 : 193), has similar rugae and costae, and is Caradoc in age.

Subfamily **AEGIROMENINAE** Havlíček 1961

Genus ***SERICOIDEA*** Lindström 1953

Sericoidea abdita Williams

(Pl. 9, figs. 3, 6)

Figured specimens (measurements in mm.)

	Length	Width
Interior of brachial valve (BB.30587) . . .	1·7	—
Interior mould of brachial valve with shell material adhering (BB.30588)	—	—

Horizon and locality. Tandinas shales, on the shore by the powerhouse 100 yds. west of the pier, Careg-onen. N.G.R. 58208193.

Discussion. Specimen BB.30587 shows the pattern of septules characteristic of this species, three pairs of lateral septules and a narrow, more prominent median septule. BB.30588 shows the cardinalia but is not complete enough to show the septules.

Superfamily **STROPHOMENACEA** King 1846

Family **LEPTAENIDAE** Hall & Clarke 1892

Genus ***LEPTAENA*** Dalman 1828

Leptaena sp.

(Pl. 10, figs. 3–6)

Description. Outline semicircular, slightly auriculate; pedicle valve with concave visceral disc bounded by a sharply raised ridge passing to a sharp geniculation; interarea apsacline, extending the width of the valve and about one-fifteenth as long as wide, delthyrium enclosing an angle of about 135°, open, pseudodeltidium not observed; brachial valve with flat visceral disc, bounded by rounded depression before the geniculation; interarea narrower than on the pedicle valve; notothyrium covered by a conspicuous convex chilidium with a median depression; interior of pedicle valve with teeth as narrow outgrowths from the hinge-line, elongated parallel to it, dental lamellae not seen, muscle scars elliptical in outline, with lanceolate adductor scars enclosed by diductors, the latter separated by a septum anteriorly; brachial interior with bilobed cardinal process tapering forwards to a point, the outer edges parallel and the inner ones diverging at 60°, sockets bounded by vague ridges forming the posterior edge to the muscle scars and uniting with a low median ridge to produce an anchor-like structure, with the median ridge passing into a short sharp median septum just before the edge of the disc, which is raised and crossed at intervals by radial grooves.

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of pedicle valve (BB.30591) . .	10·3	19·6 (est.)
Internal mould of brachial valve (BB.30592) .	—	—
Internal mould of brachial valve (BB.30593) .	—	—

Horizon and locality. Llanbabo Formation, Llanbabo Church Grits, 180 yds. east of Fferam-uchaf, Llanbabo. N.G.R. 36548673.

Discussion. The material compares well with that from the Derfel Limestone (Whittington & Williams 1955 : 419, pl. 39, figs. 86–90). There is no septum preserved between the lobes of the cardinal process in the Angelsey specimens, and their exteriors are unknown.

Genus ***DACTYLOGONIA*** Ulrich & Cooper 1942

Dactylogonia sp.

(P. 10, figs. 7–8)

Description. Brachial valve incomplete, broken along a growth line, possibly along a line of geniculation; slightly concave in longitudinal view, almost plane in anterior view; outline semi-circular, slightly alate, hinge-line straight, the greatest width; interarea very short, wide, anacline, notothyrium apparently lacking a chilidial cover; ornament of very faint concentric rugae, developing at about 3 mm. from the umbo, costellae if present too fine to be preserved; cardinal process short, bilobed, uniting with a low median ridge that bifurcates anteriorly; socket ridges diverging at 110° to each other, adpressed to the valve surface, bounding sockets which are not raised above the general interior; muscle scars bounded by a series of septa, two prominent sub-median septa parallel to each other becoming thickened and diverging at their posterior ends, separated by a slot from low thick diverging septa, which are separated from the socket ridges by a narrow depression; anterior ends of the sub-median septa separated by two triangular raised areas, between which is a thin median septum; inner surface outside the septa covered by a series of coarse pustules.

Figured specimen. Internal and external moulds of an incomplete brachial valve (BB.30596a–b).

Horizon and locality. Nantannog Formation, fine sandstones and shales 190 yds. south-east of Fferam-uchaf, Llanbabo. N.G.R. 36518657.

Discussion. Without more material it is impossible to place this specimen more exactly. The pattern of septa recalls those of *Dactylogonia* (cf. Cooper 1956 : pl. 225, fig. 4), though the septa here are nearer the socket ridges, and are separated only by narrow slots. The three pairs of raised areas together form a rim, locating within it the visceral mass of the animal. The slots between the septa were probably for the passage of the various *vascula*, the *vascula media* between the anterior pair, and the *vascula myaria* posterior to the long prominent pair. The inner margins of the two pairs of septa slope obliquely inwards, and are probably the seats of attachment of the adductor muscle scars.

?*Dactylogonia* sp. has been described by MacGregor (1961 : 204) from the upper Llandeilo of the Berwyn mountains. His specimen does not greatly resemble that described above, the septa being weakly developed, the cardinal process large, and the pustules less distinct and drawn out radially.

Genus ***KIAEROMENA*** Spjeldnaes 1957

Kiaeromena (?) sp.

(Pl. 10, figs. 9, 10)

Figured specimens. Exterior of incomplete pedicle(?) valve (BB.30594). Exterior of incomplete brachial(?) valve (BB.30595).

Horizon and locality. Garn Formation, limestone blocks in breccia bed, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The valves are semicircular, slightly alate and geniculate, and as neither the hinge-lines and interareas nor the interiors are preserved the valves have been determined on their transverse profile and ornament. The pedicle valve is convex, with the disc slightly carinate along the midline, the brachial valve with a slightly concave disc. The ornament on both valves is of fine parvicostellae, approximately ten per mm. on the valve margins, divided into sectors by stronger costellae, of which six arise near the umbo and fifteen are present at the margin of a valve about 9 mm. long. Both types of ribs arise by implantation. There are no rugae on the disc.

Order PENTAMERIDA Schuchert & Cooper 1931

Suborder SYNTROPHIIDINA Ulrich & Cooper 1936

Superfamily **PORAMBONITACEA** Davidson 1853

Family **HUENELLIDAE** Schuchert & Cooper 1931

Subfamily **RECTOTROPHIINAE** nov.

Globular huenellids with parallel dental lamellae, and with parallel supporting plates in the brachial valve, without cardinal process.

Genus ***RECTOTROPHIA*** nov.

Diagnosis. Globular subtriangular biconvex shells with deep pedicle valve and less convex brachial valve, rectimarginate commissure and narrow hinge-line; ornament unknown.

Ventral interior with parallel dental lamellae, the muscle scars confined between them and elevated on a low pseudospondylium.

Dorsal interior with parallel, receding supporting plates, without a cardinal process, adductor muscle scars hexagonal in outline, expanding anteriorly from the anterior ends of the supporting plates.

Type species. *Rectotrophia globularis* sp. nov. from the Treiorwerth Formation.

Discussion. The Heunellidae, into which the new genus falls, at present comprises two subfamilies, the Huenellinae, without a cardinal process, and the Mesonomiinae, with a rudimentary cardinal process and recumbent brachiophore plates. Both families are also characterized by the development of a fold and sulcus, and by having non-parallel supporting plates. The disposition of the supporting plates in the new genus, together with the shape of the valves and the absence of fold or sulcus, necessitate the erection of a new sub-family.

Rectotrophia globularis gen. et sp. nov.

(Pl. 10, figs. 11–17)

Diagnosis. As for genus.

TYPE SPECIMENS (measurements in mm.)

		Length	Width
HOLOTYPE.	Internal mould of pedicle valve (Af.1436)	6·7	7·0
PARATYPES.	Internal mould of brachial valve (Af.1436)	—	6·7 (est.)
	Internal mould of brachial valve (Af.1442)	6·7	5·7

TYPE HORIZON AND LOCALITY. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

DISCUSSION. The genus is known only from a few internal moulds, from Greenly's collection, the writer having found no well-preserved specimens. As a result no mean estimates of proportions can be included in a precise specific diagnosis. The holotype is 2·8 mm. thick, and the dental lamellae are 1·7 mm. apart. In the first paratype (Af.1436) the supporting plates are 1·9 mm. apart, in the second they are 1·5 mm. apart and the adductor muscle scars are 1·9 mm. long.

Family **PORAMBONITIDAE** Davidson 1853

Genus ***PORAMBONITES*** Pander 1830

Porambonites (s.s.) sp.

(Pl. 11, figs. 1–6, 8)

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.30598a–b)	18.0	—
Internal and external moulds of brachial valve (BB.30599a–b)	20·5	23·2
Internal mould of brachial valve (BB.30600) .	13·3	12·5

HORIZON AND LOCALITY. Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor. N.G.R. 36247950.

DISCUSSION. The specimens are all disarticulated, incomplete, and have suffered some distortion. Since the species of *Porambonites* are to a large extent based on external form it is not possible to make a close comparison with any described species. In addition the fold and sulcus do not develop until the shell is well grown, and of the figured specimens only BB.30599 has a good fold.

The valves are roughly circular in shape, and so do not belong to the subgenus *Equirostra* (*Isorhynchus*). The pedicle valve is lenticular, without a swollen umbo, the brachial valve more convex. The internal features of both valves are well preserved, but only the dorsal muscle scars are visible. The adductor scars are bluntly wedge-shaped and form an arc lying anterior to the ends of the supporting plates. The diductor scars are four(?) in number forming a narrower central pair flanked by two wider scars.

Allied species, from the lower Ordovician of the Baltic are *P. bröggeri* Lamansky, *P. altus* Pander and *P. planus* Pander,

Family **CAMERELLIDAE** Hall & Clarke 1894

Subfamily **CAMERELLINAE** Hall & Clarke 1894

Genus ***CAMERELLA*** Billings 1859

Camerella sp.

(Pl. 11, figs. 7, 9–11)

Figured specimen. Complete shell (BB.30597), length 4·8 mm., width 5·1 mm., thickness 2·9 mm.

Horizon and locality. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The figured specimen is the only complete one known, the others being only fragments of smaller valves. It is sub-triangular, slightly wider than long, with both valves approximately equally convex. The dorsal fold at the anterior margin is two-thirds the width of the valve, and originates at 2·6 mm. anterior to the umbo. It comprises two bounding costae, separated by a shallow depression which corresponds to a low costa or fold in the pedicle valve. The ventral sulcus is flanked by a pair of subangular costae. A few growth lines on the pedicle valve show the outline to have been sub-circular until the fold and sulcus started to develop.

The majority of described species of *Camerella* have three or more costae developed on the fold, all the costae appearing at the same time, that is, when the fold starts to appear. *C. unicostata* (Cooper 1956 : 583, pl. 113, B, figs. 6–9) has a similar development of costae on the fold and sulcus, but has more costae on the flanks, and, at the same size, seems to be more tumid and is suboval in outline.

Suborder PENTAMERIDINA Schuchert & Cooper 1931

Superfamily **PENTAMERACEA** M'Coy 1844

Family **PARALLELELASMATIDAE** Cooper 1956

Genus ***METACAMERELLA*** Reed 1917

Metacamerella cf. ***balcletchiensis*** (Davidson)

(Pl. 11, figs. 12–14)

1919 *Camarella?* [cf. *Stricklandinia? balcletchiensis* (Dav.)]; Matley *in* Greenly : 478.

Figured specimen. Complete shell (Af.1590) length 21·1 mm., width 20·0 mm., thickness 15·0 mm.

Horizon and locality. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The only specimen so far found, a complete shell from Greenly's collection, is very similar to the Girvan species (Williams 1962 : 232). The outline is comparable, with 'false interareas' extending just over half the length of the shell, and, so far as can be seen, a very low fold on the antero-median part of the brachial valve. The ornament is also very similar, consisting of about six low rounded costae, with a wavelength of 2 mm. at 13 mm. from the umbo. The interior details are not seen and hence cannot be compared with *M. balcletchiensis*.

Order uncertain

(Pl. 10, figs. 18–24)

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal and external moulds of pedicle valve (BB.55792a–b)	18·9	18·6
Internal and external moulds of brachial valve (BB.55791a–b)	—	20·5

HORIZON AND LOCALITY. Torllwyn Formation, sandstone 50 ft. above the base of the succession on the north side of the faulted syncline, 45 yds. north of Ogof Gynfor, Llanbadrig. N.G.R. 37859490.

DISCUSSION. The valves are rostrate and convex, roughly circular in outline. The pedicle valve bears a strongly marked sulcus with a flattish floor, flanked by angular folds, and has a narrow curved interarea. The delthyrium is apparently open. The brachial valve bears a corresponding fold, and both valves are costellate, with flat-topped costellae interspersed with narrow interspaces. In the ventral interior the dental lamellae are almost parallel, the muscle scars raised on a wad of callus extending anterior to the lamellae on a pseudospondylium which is rounded at its anterior end. The dorsal cardinalia are not fully preserved, though supporting plates diverge to the floor of the valve.

The external shape and ornament of the valves suggests the syntrophiid *Rhysostrophia*, but the internal structures differ considerably, and the specimens may well belong in the Orthida.

V. SYSTEMATIC DESCRIPTION OF THE TRILOBITA

Family **ASAPHIDAE** Burmeister 1843

Subfamily **OGYGIOCARIDINAE** Raymond 1937

Genus ***OGYGIOCARIS*** Angelin 1854

Ogygiocaris selwynii (Salter)

(Pl. 12, figs. 1–2, 5–6)

1919 *Ogygia selwyni* Salter; Lake *in* Greenly : 442, 446.

DESCRIPTION. Cranidium quadrilateral, wider than long, evenly convex (*tr.*). Glabella almost as long as cranidium, sides almost parallel but slightly constricted opposite the eyes, anterior margin semicircular; evenly convex (*tr.*), slightly convex (*longit.*) with a dome-shaped anterior lobe; glabellar furrows almost obsolete; one pair faintly impressed midway along the glabella. Axial furrows weak, ending in shallow hypostomal pits; occipital ring reduced to a pair of triangular raised portions pointing inwards to the tubercle, with a narrow articulating ring formed by a faint furrow behind the triangular facets (following Harrington & Leanza's interpretation, 1957 : 177). Preglabellar field absent. Fixigenae triangular shaped areas behind the eyes. Posterior border sloping slightly backwards; posterior border furrow broad and shallow, opposite the occipital ring adaxially. Eyes semicircular, very close to and centred on the transverse midline of the glabella. Facial suture isoteliform, with the anterior branches widely divergent in front of the eyes, meeting in an even curve without any apparent acumination; posterior branches oblique backwards and outwards, sigmoidal.

Pygidium transverse, one and one-half times as wide as long; anterior margin convex forwards, postero-lateral margins convex, with the greatest curvature across the midline. Axis tapering backwards, not extending onto the posterior border and with the end rounded; probably with eight or more axial rings; narrow (*longit.*) articulating half ring. Marked anterior border. Pleural fields with pleural furrows marking more than four segments, each bearing oblique ridges near their outer ends. Border of uniform width, one-fifth the length of the whole pygidium, concave but with a convex ridge against the pleural fields. Doublure convex ventrally and of the same width as the border.

Figured specimens (measurements in mm.)

	Length	Width
Internal mould of cranidium (Af.842) . . .	distorted	
Internal mould of cranidium (Af.823) . . .	31·5	36·0
Internal mould of pygidium (Af.820) . . .	37·5	54·0 (est.)
Internal mould of pygidium (Af.821) . . .	—	—

Horizon and locality. Carmel Formation, sandstones. Af.820–823 from the scarp west of Bryn Gollen Uchaf (Bryn Gwallen of Greenly), N.G.R. 40558380; Af.842 from quarry 400 yds. north-north-west of Bryn Gollen Uchaf, N.G.R. 40508425.

Discussion. The cranidia correspond closely with that of *O. selwynii* as described by Whittard (1964 : 233) though it is difficult to recognize the glabellar furrows. In particular the anterior portions of the facial sutures diverge at the same angle, and their course close to the median suture is also similar.

Af.820, the internal mould of the pygidium differs in that the posterior border is more strongly curved across the midline than laterally, whereas the reverse is true of *O. selwynii* (Whittard 1964 : 235). Af.821 shows oblique ridges in addition to the pleural furrows.

Family **THYSANOPELTIDAE** Hawle & Corda 1847

Genus ***PROTOBRONTEUS*** Šnajdr 1960

Protobronteus greenlyi sp. nov.

(Pl. 12, figs. 3–4, 7)

1919 *Illaenus caecus* Holm (*partim*); Lake *in* Greenly : 478.

Diagnosis. A species of *Protobronteus* with no inner anterior border furrow, and an ornament of coarse terrace lines without intervening pits, transverse in alignment over the anterior part of the fixigenae.

Description. Both cranidia incomplete, probably semicircular with truncated corners. Glabella clavate, reaching to the anterior border, evenly convex (*sag.* and *tr.*); narrowest just behind the midline (*sag.*), just longer than wide; without glabellar furrows. Axial furrows convex inwards, well defined. Occipital ring not seen. Fixigenae incomplete, evenly convex (*long.*), palpebral lobe and course of facial suture not seen. Anterior border not separated from glabella mesially, but present in front of the fixigenae; anterior border furrow well defined, meeting the axial furrow in a right angle, and continuing a little way adaxially to define the anterolateral corner of the glabella. Ornament of coarse terrace lines, averaging five to eight per 5 mm., becoming crowded together on the anterior border, transverse across the glabella, borders and anterior part of the fixigenae, not preserved elsewhere.

Librigena incomplete, triangular, convex (long.), with prominent anterolateral border furrow, no posterior border furrows. Eye lobe large, semicircular. Genal spine long, circular in cross-section. Ornament of distant terrace lines, diverging on either side of eye.

TYPE SPECIMENS (measurements in mm.)

		Length	Width
HOLOTYPE.	Incomplete cranidium (In.58291) . .	28·8	—
PARATYPES.	Incomplete cranidium (In.58292) . .	—	—
	Internal mould and interior of incomplete librigena (In.58293a–b) . . .	—	—

TYPE HORIZON AND LOCALITY. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

DISCUSSION. *Protobronteus* was erected by Šnajdr (1960 : 245–246) to include only *Eobronteus reedi* Sinclair (1949 : 51–52). In this species, as in *P. greenlyi* the glabella is clavate, without any glabellar furrows, and coalesces with the anterior border. *E. curtus* Sinclair (1949 : 50–51) is very similar and could well be included in *Protobronteus* as the glabellar furrows are indistinct and the anterior border furrow fades out mesially.

P. greenlyi differs from both these species in that the inner anterior border furrow is absent (the cheek furrow of Sinclair 1949 : 51), and the ornament is differently developed. In *P. reedi* the terrace lines are longitudinal between the two border furrows, and in *E. curtus* they are not developed in the same place, only coarse punctae being present.

Family **ILLAENIDAE** Hawle & Corda 1847

Subfamily **ILLAENINAE** Hawle & Corda 1847

Genus ***ILLAENUS*** Dalman 1827

Illaenus sp.

(Pl. 12, figs. 8–13, 15)

1919 *Illaenus caecus* Holm (*partim*); Lake *in* Greenly : 478.

DESCRIPTION. Cranidium quadrangular, evenly convex (*tr.*), longitudinal convexity strong posteriorly, weak anteriorly. Glabella short and wide, with slight independent convexity (*tr.*), two-thirds the width of the cranidium. Axial furrows curve inwards for two-thirds of their length, and end in an outwards curve. Palpebral lobes one-third the length of the cranidium, situated less than their own length from the posterior margin. Posterior branches of the facial sutures short, running directly backwards, anterior branches slightly divergent. Dorsal surface of cranidium smooth.

Pygidium parabolic, the anterior margin slightly convex forwards, width four-thirds the length, convex, the inner pleural fields gently convex and the margins deflected at about 45°. Axis short, sub-triangular, with independent convexity (*tr.*), four-tenths the width of the pygidium. Axial furrows shallow posteriorly, meeting at about 60°. Short (*long.*) articulating half ring. Pleural fields with anterior borders slightly swollen, marked off by shallow depressions. Articulating facets sharply bevelled, with terrace lines extending beyond them. Rest of dorsal surface finely pitted. Doublure close to the dorsal shield, convex ventrally at its outer margin, almost half the length (*sag.*) and one-tenth the width of pygidium at anterior margin. Inner margin commencing near midline of facet (tr.), swinging in a curve gradually decreasing in radius to the midline of the pygidium, where a forward pointing cusp is found. Ventrally deflected median ridge strongly marked. Doublure bears terrace lines running parallel to its margins about 0·7 mm. apart.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Cranidium (In.58294)	—	9·9
Pygidium (In.58295)	23·7	32·7
Pygidium (In.58296)	22·6	33·5

DISCUSSION. The species resembles *Illaenus revaliensis* (Holm 1886 : 87–92, pl. 2, figs. 1–10) particularly in the shape and other features of the pygidium. The axis is similar, and the inner margin of the doublure has a forward pointing cusp at the midline. The cranidium is poorly preserved, and may possibly be a crushed and distorted cranidium of *Stenopareia* cf. *linnarssoni* (Holm), but the glabella is relatively wider, the palpebral lobes are much larger, and the anterior margin seems to be sharply truncated.

Genus ***STENOPAREIA*** Holm 1886

Stenopareia cf. ***linnarssoni*** (Holm)

(Pl. 12, figs. 14, 16–23)

1919 *Illaenus caecus* Holm (*partim*); Lake *in* Greenly : 478)

DESCRIPTION. Cranidium quadrangular, the frontal area domed, strongly and evenly convex (*long.* and *tr.*). Glabella with slight independent convexity (*tr.*), half the length of cranidium. Two pairs of oval muscle scars between the axial furrows, the anterior pair indistinct. Axial furrows poorly defined on dorsal, but well defined on ventral surface, extending forwards half the length of cranidium, widening in their anterior half to be well defined on the ventral surface. Palpebral lobes less than one fifth the length of cranidium, less than their own length from the posterior border. Posterior braches of facial suture short, straight, running diagonally outwards, anterior branches straight, converging slightly forwards. Glabella and fixigenae with smooth dorsal surfaces, frontal margin with faint terrace lines on the ventral surface.

Librigena twice as long as wide, tapering to a point anteriorly, with vertically deflected border present anteriorly. Genal angle very broadly rounded.

Rostral plate triangular, anterior margin gently convex outwards, the posterior margins concave rearwards, meeting in a central cusp with an angle of less than 90°. Ventral surface with terrace lines.

Pygidium semi-oval, just over half as long as wide, weakly convex except at the sides where almost vertically deflected. Axis one-third the anterior width, undefined posteriorly, evenly convex (*tr.*). Axial furrows shallow, only seen at anterior margin. Dorsal surface smooth. Articulating facets convex, almost vertical. Doublure lies close to the dorsal surface, with a faint median ridge, anterior margin monocuspid(?).

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Cranidium (In.58297)	15·5	18·6
Cranidium (In.58298)	—	14·6 (est.)
Librigena (In.58299)	19·7	—
Rostral plate (In.58300)	8·9	22·6
Pygidium (In.58301)	23·4	42·4 (est.)
Pygidium (In.58302)	13·5	22·5

HORIZON AND LOCALITY. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

DISCUSSION. The cranidium is very similar to that of *Stenopareia linnarssoni* (*Illaenus linnarssoni* Holm *in* Warburg 1925 : 115–123, pl. 2, figs. 14–18). The glabellar proportions and the axial furrows are the same, with an anterior swelling of the furrows. The palpebral lobes are the same size and equally far back. The pygidia are approximately similar in proportion; the inner margin of the doublure is unknown, though it also has a ventrally deflected median furrow. The facets are narrow and rounded in both cases, but the axis is relatively narrower in the Anglesey specimens. *Stenopareia camladica* Whittard (1961 : 216–217, pl. 30, figs. 10–13) has a similar cranidium, but the axial furrows are poorly preserved, and the pygidium is differently proportioned in the Shropshire species.

Family **HARPIDAE** Hawle & Corda 1847

Genus ***SELENOHARPES*** Whittington 1950

Selenoharpes (?) sp.

(Pl. 13, figs. 1–2, 5–6)

DESCRIPTION. Outline of cephalon oval; greatest width probably behind the occipital ring.

Glabella tapering forwards, width at its base seven-ninths of its length, rounded anteriorly; sharply convex and carinate, in height equal to its width; in lateral profile becoming vertical anteriorly. Basal lobes triangular, very vague, one-third the length of the glabella, marked by shallow furrows running inwards and backwards. Axial, preglabellar, and occipital furrows all shallow. Occipital ring one-ninth length of the glabella, bent up with it.

Pre-glabellar field one-third length of the glabella, sloping anteriorly. Eye tubercles prominent and elevated above the cheeks, opposite the anterior one-fifth of the glabella. Eye ridges broad, running directly inwards. Genal ridges fine, running outwards and backwards to the girder. Alae one-third the length of the glabella, depressed, marked by semicircular alar furrows. Cheek lobes bent down anterolaterally and laterally. Posterior border with sharply raised convex rim, continuous with a similar rim on the inward side of the prolongations. Cheek roll not separable from the cheeks. Brim equal in width anteriorly to the glabellar length, convave, with a row of prominent pits just inside the rim marking the inner edge of a downward bevel round the rim. Girder smooth, with prominent pits forming a single row on both sides; girder possibly meeting the internal prolongations. Glabella and alae smooth; preglabellar field and cheek lobes anterior and lateral to the eyes with radiating ridges with fine pits between them; on the rest of the cheeks and on the brim are similar fine pits but without ridges or arrangement.

Figured specimen. Incomplete cranidium (In.58303).

Horizon and locality. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The two closest genera are *Selenoharpes* and *Aristoharpes*, the former of Middle Ordovician (post-Llandeilo) age and the latter of Llandovery age. In *Selenoharpes* the glabella tapers forwards, the eye ridges are prominent and genal ridges are present. In *Aristoharpes* the glabella is sub-parallel sided, eye ridges are weak and genal ridges absent. It also has much smaller alae than *Selenoharpes*, which are one-quarter the length of the glabella compared with one-half. There is thus some doubt as to where to place these specimens, which compare closely with *Selenoharpes*, except for the smaller alae, a difference that is probably trivial. The specimens are certainly not conspecific with the type species, *S. youngi* (Reed) from the lower Caradoc of Girvan, in which the brim is convex upwards.

Family **TRINUCLEIDAE** Hawle & Corda 1847

Subfamily **CRYPTOLITHINAE** Angelin 1854

Genus ***BERGAMIA*** Whittard 1955

Bergamia (?) sp.

(Pl. 13, figs. 3–4, 9, 13)

Description. Cephalon twice as broad as long. Glabella pyriform, swollen, tapering markedly posteriorly, second and third furrows fairly well marked, pit-like in form; well marked alae bounded laterally by deep furrows, ending laterally against the posterior border in well marked knobs; glabellar furrows not well marked against the alae. Genae swollen, crossed by a ridge running obliquely back from the front of the glabella to the genal angle. Occipital ring very narrow, arched and convex posteriorly; posterior borders from a narrow sharp ridge posterior to a wide shallow furrow. Glabella and genae posterior to the ridge bear a strong reticulate pattern, becoming faint towards the front of the glabella. Fringe of uniform width throughout except at the genal angle; pits sunk in deep radial sulci; girder not seen in any of the specimens; sulci number eighteen on each side of the centre-line, with up to four pits in each; interradial sulci numbers i and ii present; some twin pits.

Thoracic segments not well preserved; axis strongly convex with axial rings convex posteriorly; pleural regions with strong oblique pleural furrows; pleural spines strong and directed posteriorly.

Pygidium over twice as wide as long, triangular in outline; axis tapers at 30° with at least five axial rings, well defined and strongly arched; pleural lobes divided by at least four faintly marked oblique interpleural furrows; anterolateral angles bevelled as an articulating facet; posterior margins with a broad border of uniform width, slightly raised over the centre-line.

FIGURED SPECIMENS. Counterpart moulds of cranidium and pygidium (In. 58304a–b). Length of cranidium (sag.) 3·4 mm., width 7·0 mm. Length of pygidium 1·7 mm., width 4·2 mm.

Counterpart moulds of complete dorsal carapace (In. 58305a–b). Length (sag.) 2·5 mm.

Ventral mould of dorsal carapace (In. 58306) Distorted.

HORIZON AND LOCALITY. Shales, *D. bifidus* zone, quarry 100 yds. north of Gwredog-uchaf farm, Rhodogeidio. N.G.R. 40488628.

DISCUSSION. The preservation of the specimens, in particular of the fringe, is not good enough to make a certain generic identification. However, the simplicity of the fringe suggests that the specimens belong to *Bergamia*, which ranges from the uppermost Arenig through the Llanvirn, and possibly into the Caradoc (Whittard 1955 : 31). The species resembles *B. rhodesi* Whittard (1955 : 32) in the arrangement of the pits on the fringe. The smallest specimen illustrated (Pl. 13, fig. 3) is a meraspid of probably degree two. There is little difference in characters from the larger specimens.

Family **RAPHIOPHORIDAE** Angelin 1854

Genus ***AMPYX*** Dalman 1827

Ampyx sp. (1)

(Pl. 13, fig. 8)

1919 *Ampyx* cf. *domatus* (Angelin); Lake *in* Greenly : 446.
1955 *Ampyx* sp.; Whittard : 17.

FIGURED SPECIMEN. Cranidium (Af. 824). Length 9·0 mm., width 12·4 mm.

Horizon and locality. Carmel Formation, sandstones on the escarpment 300 yds. west of Bryn Gollen Uchaf. N.G.R. 40558380.

Discussion. This specimen remains the only one collected from the basal grits, and there is nothing that can be added to Whittard's opinion that it probably belongs to an undescribed species.

Ampyx sp. (2)

(Pl. 13, figs. 7, 10–12)

1919 *Ampyx nasutus* Dalman; Lake *in* Greenly : 433.

Description. Cranidium quadrilateral in outline, length four-tenths the width, the anterior border very well developed. Glabella pyriform, widest near the anterior end and broadly rounded in front, one-third to one-quarter the width of the cranidium in front, tapering to the occipital ring, exceptionally weakly swollen, overhanging only part of the preglabellar field. One pair of glabellar furrows almost isolating long narrow lobes, the furrows running back parallel to the axial furrows, starting just anterior to the transverse midline of the glabella; alae (cf. Whittard 1955 : 15) crescentic, starting anterior to the glabellar furrows and extending backwards to meet the posterior border furrow, axial and alar furrows faint; glabellar spine at least half as long as the cephalon, circular in cross section, possibly concave dorsally. Fixigenae triangular, gently convex. Facial suture runs in a gentle sigmoidal curve convex outwards as it crosses the posterior border, convex inwards forwards of this and again convex outwards in its anterior third. Occipital ring narrow, occipital furrow shallow, both convex backwards. Posterior border furrow broad and shallow, running obliquely outwards and backwards, but sweeping forwards again near the genal angle; posterior border widening laterally. Pre-glabellar field comparatively long, about one-sixth the length of the cephalon, flattened.

Thorax of six segments, broad and flat. Axis convex, axial rings each with a shallow groove defining small lobes at each side. Pleurae parallel-sided, each with an oblique furrow curved forward at the tip, sharply deflected ventrally at prominent fulcral processes which appear as tubercles. First or macro-pleurae longer than the others with outer margins not deflected but sloping backwards and out to the fulcrum. Other pleurae with blunt terminations.

Pygidium triangular, twice as wide as long. Anterior margin straight, postero-lateral borders slightly convex, deflected, with terrace lines parallel to the margins. Axis convex, with narrow articulating half-ring, tapering from one-fifth the width of the pygidium anteriorly to a point at the posterior end, occasionally a few axial rings present. Pleural lobes smooth, except for strongly developed anterior borders, marked off by sharp furrows running obliquely backwards and outwards, becoming concave forwards laterally to meet the anterolateral angle of the pygidium. Prominent fulcral tubercle at the inner end of the articulating facet.

Figured specimens (measurements in mm.)

	Length	Width
Internal and external moulds of cranidium (In. 58307a–b)	16·0	35·6 (est.)
External mould of cranidium (In.58308)	—	—
Internal mould of thoracic segments and pygidium (Af.3653)	16·3	19·3
External mould of pygidium (In.58309)	7·0	16·8 (est.)

Horizon and locality. Tandinas shales, by the track leading down to the quarry, and on the shore behind the power house, at Tandinas quarry, Careg-onen. N.G.R. 58248187.

Discussion. The species is similar to *A. linleyensis* Whittard of the Shelve area (*D. bifidus* zone), but differs in having a short, weakly swollen glabella, a pre-glabellar field, and having terrace lines on the pygidium. *A. salteri* Hicks (*D. extensus* zone?) also has terrace lines to the pygidium, but lacks a pre-glabellar field.

Family **CHEIRURIDAE** Salter 1864

Subfamily **CHEIRURINAE** Salter 1864

Genus ***CERAURINELLA*** Cooper 1953

Ceraurinella sp.

(Pl. 13, figs. 14–22)

Description. Cranidium roughly triangular in outline, broader than long. Glabella evenly convex (tr.), gently convex (sag.) becoming more convex along the anterior lobe. Length equal to the maximum width, the latter across the anterior lobe, sides slightly tapering towards the occipital ring, front margin convex forwards. Three pairs of narrow well marked glabellar furrows; 1p inclined obliquely backwards, bent back to join the occipital furrow nearer the midline than the axial furrows; 2p and 3p parallel to each other, curving obliquely backwards and crossing one-third the width of the glabella (*tr.*). Basal lobes with independent convexity, one and a half times the length (*exsag.*) of the second and third lobes; the latter subequal in length without independent convexity. Occipital furrow not well seen, shallow. Fixigenae triangular convex, eye lobe on the highest part, opposite and close to the second glabellar lobe, equal in length to that lobe (*exsag.*). Anterior part of fixigenae parallel sided, anterior branch of facial suture running in to meet the axial furrows just in front of 3p glabellar furrows. Posterior branch of facial suture runs transversely out from the eye, and curves round to meet the anterolateral border of the cranidium. Posterior border furrows deep and wide, bending sharply forwards to meet the lateral border furrow. Posterior border widening laterally towards genal spine, length of latter unknown. Glabella and borders smooth, fixigenae coarsely tuberculate. Librigenae unknown.

Hypostome slightly longer (*sag.*) than maximum width (*tr.*) across anterior wings, tapering backwards to a width at the posterior border half the maximum. Median body convex (*sag.* and *tr.*) widest in front of anterior wings. Anterior, lateral and posterior border furrows broad and shallow. Middle furrows faint, running in from opposite shoulders to end in shallow pits. Posterior lobe crescentic, independently convex where marked off by the middle furrows. No anterior border medianly. Anterior wing slopes steeply dorsoposteriorly, tip narrow and spine-like. Lateral border commences opposite anterior wing, widens rapidly to prominent and sharp shoulder (in ventral view) which is just less than half the way back (*exsag.*) from the anterior border, continuous with the posterior border. Short denticle or spine on the posterolateral corners, posterior border straight. Posterior wing not seen. Entire surface smooth.

Thorax of unknown number of segments. Axis arched, most sharply convex over the midline, length (*sag.*) one-fifth the width, width one-quarter that of the whole segment. Anterior margin convex forwards over the midline, concave forwards laterally above the apodemes, which are deflected ventrally (no articulating half-ring seen). Inner part of pleura horizontal, divided in two by a furrow parallel to the axial furrow, the inner part being one-third the width of the whole, and crossed by a diagonal furrow, the outer part bent abruptly ventrally and forming a gradually tapering pleural spine. No ornament on the segments.

Pygidium poorly preserved. Convex axis with four axial rings, or three axial rings and an articulating half ring. Margin not preserved, except for one long tapering spine probably commencing opposite the second axial ring and curving backwards towards its tip. No ornament present.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Incomplete glabella (In.58310)	—	8·7
Incomplete glabella (In.58311)	—	10·3
Incomplete cranidium (In.58312)	13·6	—
Hypostome (In.58313)	—	—
Hypostome (In.58314)	7·9	5·4
Hypostome (In.58315)	—	9·1
Thoracic segment (In.58316)	—	—
Thoracic segment (In.58317)	—	—
Incomplete pygidium (In.58318)	—	—

HORIZON AND LOCALITY. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

DISCUSSION. The specimens are assigned to *Ceraurinella* since the eyes are opposite the 2p lobes and near the glabella, the genal spines though not complete are short, the pygidium has the long spines typical of that genus (and *Ceraurus*), and the thoracic segments and hypostome also are of the same type. The species described by Cooper (1953 : 29–30) and by Whittington & Evitt (1953 : 62–70) differ in their ornament, which is more pervasive, and possibly also in other minor details. None of the species of *Ceraurus* (Raymond & Barton 1913; Barton 1913) corresponds. *Ceraurinella*? sp. has been recorded by Whittington from the Derfel limestone (*in* Whittington & Williams 1955 : 422–423, pl. 40, figs. 102, 107 and 111), but the two species are not the same, as in his figures the eyes, not preserved, cannot have been farther back than opposite the 3p glabellar lobes, and the 3p lobes seem to be longer (*sag.*) than the others.

Subfamily **SPHAEREXOCHINAE** Öpik 1937

Genus ***SPHAEREXOCHUS*** Beyrich 1845

Sphaerexochus sp.

(Pl. 14, figs. 1–2)

DESCRIPTION. Cranidium only preserved, distorted by flattening, crescent shaped in outline, original convexity not known. Glabella subcircular to pentagonal in outline, widest opposite the second glabellar furrow (2p). Occipital ring narrower than the glabella at its maximum, one-eighth of glabella length (*sag.*), convex, posterior margin concave backwards. Occipital furrow broad and deep, uniformly curved throughout. First glabellar furrows (1p) transverse with a gently concave backwards curve, curving sharply at their inward ends towards the occipital furrow, running to meet it in another gentle curve convex sagittally. The first lateral glabellar lobes isolated, subquadrate in outline, possibly without independent convexity, four-ninths the length of the glabella (*sag.*), approximately two-ninths its width. Second glabellar furrow (preserved only on one side) very short, straight. Second glabellar lobe one-half length of the first. No third glabellar lobes or furrows. Anterior border not preserved. Fixigenae small, triangular, convex. Palpebral lobe very narrow, opposite to 1p furrow, two-thirds the length of the first lobes. Facial suture not seen forward of the eye. Posterior branch runs outwards and then backwards to meet the posterior border at right angles. Posterior border equal in width to the occipital ring at its inner end, widening towards the genal angle. Posterior border furrow concave forwards, dying out towards the genal angle.

FIGURED SPECIMEN (measurements in mm.)

	Length	Width
Cranidium (In.58319)	6·0 (sag.)	9·5

HORIZON AND LOCALITY. Tandinas shales, on the shore by the powerhouse, 100 yds. west of the pier, Careg-onen. N.G.R. 58208193.

DISCUSSION. The specimen differs from all described species of *Sphaerexochus* by having two pairs of lateral glabellar furrows. *S. bilobatus* (Whittard 1958 : 110) has only the basal pair developed, otherwise three pairs seem to be the rule. The preservation of the specimen has resulted in accentuation of the anterior furrow on one side, and its obliteration on the other. It is possible, though unlikely that a third pair of furrows may be present, but obliterated.

Family **PLIOMERIDAE** Raymond 1913

Subfamily **PLIOMERINAE** Raymond 1913

Genus ***PLIOMEROPS*** Raymond 1905

Pliomerops sp.

(Pl. 14, figs. 3–4, 6–7)

DESCRIPTION. Cranidium incomplete. Glabella quadrangular, expanding forwards from the occipital ring to midway between the pre-occipital and middle furrows, forwards of this having a domed margin, slightly flattened in the centre. Dorsal furrows deeply impressed. Pre-occipital furrows (1p) commencing at one-third the length of the glabella forwards from the occipital ring, running obliquely inwards and backwards for one-quarter the width of the glabella, at that point turning abruptly to run slightly forwards, finally curving round to point obliquely backwards at their inner tips, which are separated by one-eighth the width of the glabella. Middle furrows (2p) commencing just forwards of two-thirds the length of the glabella, running inwards and backwards to as near the midline as the pre-occipital furrows, the tips of the inner ends of the two pairs of furrows being much closer together than their outer ends. Anterior furrows (3p) located on the anterior margin, half way between the midline and the anterolateral corner of the glabella, faint and short, being little more than indentations of the margin. Rear two pairs of glabellar lobes with independent convexity. Axial furrows of the same depth as the glabellar furrows, curving smoothly into the anterior border furrow. Occipital furrow convex forwards at centre, becoming concave forwards towards the axial furrows. Occipital ring not completely preserved, lengthening (sag.) towards the midline. Anterior border strongly arched dorsally over the midline, widest at the midline and at the anterolateral angles of the cephalon. Fixigenae incompletely preserved.

Hypostome shield-shaped, anterior border convex, lateral and posterior borders with a sigmoidal curve ending in a posterior point, slightly wider than long, almost flat. Middle body of same shape. Anterior lobe produced into lateral wings, posterior lobe crescentic, defined by middle furrows commencing just behind the wings, broad and shallow, curving gradually inwards. Anterior border poorly preserved, widest at the anterior wings. Lateral and posterior borders of uniform width except at their anterior ends. All border furrows wide and shallow.

Pygidium with shape of an extremely taut bow, just longer than wide, anterior margin very convex forwards. Convex (*tr.*), the margins deflected ventrally at angles up to 90°, almost flat (*sag.*), but convex (*exsag.*). Axis convex, of five flat-topped (*sag.*) axial rings, tapering backwards, followed by a terminal axial piece one and one half times as long as the rings, parallel sided for half its length and tapering to a point in the posterior half. Pleural portions of five pleural lobes, without a border, each lobe widening to the margin and truncated to produce a smooth lateral and posterior border; the last pair surrounding the axis and separated by a median furrow.

Figured specimens (measurements in mm.)

	Length	Width
Incomplete cranidium (In.58320)	16·5	—
Hypostome (In.58321)	14·5	—
Pygidium (In.58322)	39·0	—
Internal mould and interior of pygidium (In. 58323a–b)	—	17·0 (est.)

Horizon and locality. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The above descriptions are of isolated pieces from the limestone blocks, and, assuming they belong together, they are assigned to the genus *Pliomerops* Raymond on the basis of the diagnosis given by Harrington (*in* Moore 1959 : *O* 440). The anterior border is not denticulate, there is no median indentation of the glabella, and the terminal axial piece is long and enclosed. The cranidium resembles that of *P. canadensis* (Billings) illustrated in the Treatise (Moore 1959 : fig. 345, 2b) but the pygidia do not. As far as can be seen, most of the described species of *Pliomerops* have short terminal axial pieces and usually a denticulate margin, though the diagnosis in the Treatise (Moore 1959 : *O* 440) states that the terminal axial piece is long. Reed (1906 : 153, Plate XIX, fig. 16) figures a pygidium very like this as *Pliomera* sp.

B. N. Cooper (1953) has described a pliomerid from Virginia, *Pliomerella americana*, which is somewhat similar to the Anglesey specimens. The pygidium appears to be identical, to judge from Pl. 10, fig. 4 of his paper. This is a crushed specimen, but the long axial piece is apparently enveloped by the posterior pleurae. Another pygidium is illustrated in fig. 1 of the same plate, in which the terminal axial piece is quadrate and reaches the posterior margin, though it may be that the posterior part is missing, and the caption states that the specimen is incomplete. Cooper's text does not indicate whether the axial piece is enveloped or not, and the specimen of his Pl. 10, fig. 1 is re-illustrated on p. *O* 445 of the Treatise (Moore 1959 : fig. 348, 2b) as being in fact complete. The accompanying text in the Treatise (Moore 1959 : *O*445) states that a pygidium of this sort is diagnostic of *Pliomerella*. The genus was erected by Reed (1941 : 269) for trilobites with two pairs of glabellar furrows 'combined with some characters of *Pliomera*', but he did not describe a pygidium. It is thus probable that *Pliomerella americana* Cooper does not belong to *Pliomerella*, but possibly to *Pliomerops*, though there is no sign in Cooper's figures of the anterior glabellar furrows, nor does he describe them in the text.

Subfamily **PLACOPARIINAE** Hupé 1953

Genus ***PLACOPARIA*** Hawle & Corda 1847

Placoparia sp.

(Pl. 14, fig. 5)

1919 *Placoparia* sp.: Lake *in* Greenly : 466.

Figured specimen. Dorsal carapace (Af.1319). Length 23·1 mm.

Horizon and locality. Shales of the *Gl. teretiusculus* zone, 80 yds. north of the streamlet, on the shore at Porth-y-gwichiaid (Greenly 1919 : 466). N.G.R. 48799160.

Discussion. The species *P. zippei* (Boeck) has recently been divided into two species, *P. zippei* and *P. barrandei* Prantl & Šnajdr, differing in a number of small features, including the glabellar shape, details of the glabellar and occular furrows, and the development of vincular notches (Whittard 1966 : 283–284). *P. barrandei* itself is a synonym of *P. cambriensis* Hicks (1875 : 186, pl. 9, figs. 1–2) (Dr. W. T. Dean, personal communication).

The Anglesey specimen belongs more probably to *P. cambriensis*, as the glabella is quadrate rather than trapezoidal in outline, though the evidence of the other features is equivocal, probably due to crushing of the specimen.

Family **CALYMENIDAE** Burmeister 1843

Subfamily **CALYMENINAE** Burmeister 1843

Calymenid undet.

(Pl. 14, figs. 8–9, 12–13)

Figured specimens (measurements in mm.)

	Length	Width
Hypostome (In.58324)	6·7	5·6
Pygidium (In.58325)	9·3	11·5

Horizon and locality. Garn Formation, limestone blocks in breccia bed, Porth Padrig, Mynachdy. N.G.R. 30539279.

Discussion. The material found consists of one complete pygidium, and one complete and one incomplete hypostome. It is assumed that they all belong to one species.

The pygidium is oval in outline, and strongly convex. The axis gradually tapers backwards, not reaching the posterior border, with six well defined axial rings, a terminal piece and an articulating half ring. The pleural portions show deep pleural furrows with much shallower interpleural furrows, extending to the margin but becoming much fainter on the border. The border is marked by faint depressions running from the tip of the axis to the anterior margins. There are well defined and almost vertically deflected articulating facets, with the foremost pleural groove extending onto them. In posterior view the lateral and posterior margins show a strongly marked arch across the midline. The entire surface, except for the articulating facets and the furrows, is finely tuberculate.

The hypostome is longer than wide, rectangular in outline. The middle body is parallel-sided, with faint diagonal middle furrows dividing off a crescentic posterior lobe, convex longitudinally and sharply convex transversely, without a raised central portion to the anterior lobe. The anterior border is flexed ventrally, continuous with large anterior wings. The lateral borders have a wide gently curved notch extending from the anterior wings to opposite the anterior end of the posterior lobe. The lateral and posterior borders behind this are wide and flat, produced into points almost one-third of the length of the hypostome, separated by a deep median notch extending to the end of the middle body. The tips of the points and the notch are all sharp, each with an angle of about 50°.

Subdivision of the Calymeninae is based mainly on cephalic characters, so it is not possible to give a generic designation. The upper Ordovician calymenid species have been assigned to five different genera by Shirley (1936 : 400), and of these *Platycalymene*, *Gravicalymene* and *Flexicalymene* agree in their pygidal characters. *Flexicalymene* is the closest in character, and the pygidium described and figured by Shirley (1936 : 406, pl. 29, fig. 7) looks similar, though it is more angular in outline.

Family **HOMALONOTIDAE** Chapman 1890

Subfamily **EOHOMALONOTINAE** Hupé 1953

Genus ***NESEURETUS*** Hicks 1872

Neseuretus monensis (Shirley)

(Pl. 14, figs. 11, 16)

1919 *Calymene parvifrons* Salter; Lake *in* Greenly : 442, 446.
1919 *Calymene tristani* Brongniart; Lake *in* Greenly : 442.
1936 *Synhomalonotus monensis* Shirley : 401.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Internal and external moulds of pygidium (In. 58326a–b)	16·9	21·0 (est.)
Internal mould of pygidium (In. 58327) . .	distorted	

HORIZON AND LOCALITY. Carmel Formation, sandstones; In. 58326a–b from 440 yds. north of Ty-hen, Treiorwerth, N.G.R. 35767891; In. 58327 from 120 yds. north-west of Chwaen-bach, Llanerchymedd, N.G.R. 39468378.

DISCUSSION. Shirley described this species from specimens in Greenly's collection (G.S.M. Af. 930–2). The thorax, librigenae and pygidium were not represented in the collection, so only the cranidium was described. Pygidia have been found from the same horizon, and give additional information on the species. The specimen from Chwaen-bach is distorted, and the description is based on that from near Ty-hen (In. 58326).

The pygidium is broader than long, roughly elliptical but with the anterior margin more strongly curved than the borders. The axis bears an articulating half ring and furrow. The axis is funnel-shaped, the tapering portion containing at least six rings, followed by an almost cylindrical portion terminating in a rounded end not quite reaching the posterior margin. The pleural lobes are gently convex, and bear six rounded unfurrowed pleurae, separated by well marked interpleural furrows. The border is sharply rounded, but the form of the doublure is unknown. The pygidium from Chwaen-bach shows pleural furrows which may be the result of crushing.

Family **LICHIDAE** Hawle & Corda 1847

Subfamily **TETRALICHINAE** Phleger 1936

Genus ***AMPHILICHAS*** Raymond 1905

Amphilichas sp. (1)

(Pl. 14, figs. 10, 14–15, 17)

DESCRIPTION. Cranidium roughly pentagonal, strongly bent down at the anterior and posterior lateral corners. Glabella rounded, axe-shaped, as broad as long, strongly convex, overhanging in front. Frontero-median lobe prominent, expanded in front to more than twice its basal width; anteriorly strongly convex; anterior lateral angles rounded; posteriorly parallel sided and less convex. First lateral (longitudinal) furrows run inwards towards centre of lobe, curving steadily round to become parallel and meet the occipital furrow at right angles. Lateral lobes gently convex, a little less elevated than the median lobe; bluntly pointed in front, strongly bent down with the antero-median lobe; posterolateral angles extend considerably further back than the median lobe. Axial furrows as strong as longitudinal furrows, posteriorly parallel to them, diverging slightly in front of the eyes. Occipital furrow straight and horizontal behind median lobe, directed obliquely backwards behind the lateral lobes, and less obliquely behind the fixigenae. Occipital ring not completely preserved but possibly widest behind the median lobe. Fixigenae posteriorly equal in width to the lateral lobes, narrowing to less than half that width opposite the eye; expanding in front of the eye; expanding in front of the eye but not completely preserved. Course of facial suture only seen round eye, running outwards behind it. Palpebral lobe semicircular, convex inwards; its length is one-fifth that of the glabella and its posterior end level with the occipital furrow. Entire cranidium, except for the furrows, covered with tubercles of varying size, irregularly placed.

Hypostome oval in outline, broader than long. Posterior border broad, posterior margin indented. Middle body circumscribed. Posterior lateral lobes well defined by median furrows running inwards slightly posteriorly with short bifurcations at their inner ends. Lateral borders broad, with short triangular wings opposite the posterior border furrow. Anterior border appears to be lacking. Anterior part of middle body pitted; anastomosing ridges or terrace lines on remainder of surface.

FIGURED SPECIMENS (measurements in mm.)

	Length	Width
Incomplete cranidium (In.58328)	14·9	—
Hypostome (In.58329)	5·8 (sag.)	7·9

HORIZON AND LOCALITY. Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy. N.G.R. 30539279.

DISCUSSION. No thoracic segments have been found, and the only remains of pygidia so far found are too incomplete to describe; they only show the typical development of tubercles. The cranidium shows similarities to *A. wahlenbergi*

Warburg from the *Leptaena* Limestone in Dalarne, and also to *Lichas* (*Amphilichas*) *hibernicus* (Portlock) (Reed 1906 : 106, pl. 15, fi. 1 *non* 2–3).

Amphilichas sp. (2)

(Pl. 14, figs. 18–19)

DESCRIPTION. Outline possibly semicircular, weakly convex both longitudinally and transversely, probably crushed. Frontero-median lobe convex, expanding forwards to over twice its posterior width; the longitudinal furrows being parallel posteriorly and curving outwards to diverge at more than 90° where they meet the axial furrow, not reaching the occipital furrow but ending in a pit. Tricomposite lobe widening very slightly forwards, at its posterior end the same width as the median lobe posteriorly; axial furrows concentric with the longitudinal furrows but with smaller radius of curvature. Fixigena incomplete, narrow, posterior to the eye less than half the width of the tricomposite lobe, cut into by the eye lobe, which is one-fifth the length of the cranidium. Only a fragment of the occipital ring preserved. Surface evenly pitted.

FIGURED SPECIMEN (measurements in mm.)

	Length	Width
Incomplete external mould of cranidium (Af. 3000)	17 app.	—

HORIZON AND LOCALITY. Tandinas shales, by the track 50 yds. west of Tandinas quarry, Careg-onen. N.G.R. 58248187.

DISCUSSION. There appear to be no basal lobes, so that the specimen belongs to *Amphilichas*, although there is little to compare closely with *Amphilichas* sp. (1) from Porth Padrig.

Family uncertain

Genus ***MONELLA*** nov.

DIAGNOSIS. Genus similar to *Glossopleura* Poulsen, but differing in having more strongly marked glabellar furrows, the anterior ends of the palpebral lobes not touching the glabella, and eleven (compared with eight) thoracic segments.

TYPE SPECIES. *Monella perplexa* sp. nov. from the Carmel Formation.

DISCUSSION. The specimens assigned to the new genus were referred by Lake (*in* Greenly 1919) to *Ogygia*, but certainly do not belong to the suborder *Asaphina*. The thorax consists of eleven segments and the glabella is distinctly furrowed, a combination of characters that is quite different from any contemporary trilobites, but generally characteristic of the Order *Corynexochida*, though the rostral plate and hypostome have yet to be found. The glabella is clavate and reaches the anterior margin, the eyes are large and semicircular, with prominent palpebral lobes, though eye ridges are not present. The closest genera are found in the family Dolichometopidae, of the order *Corynexochida*. *Athabaskiella* has a similar cephalon, but a smaller pygidium with only four segments differentiated in the pleural regions and fewer in the axis. *Bathyuriscus* has smaller eyes which are not semicircular, and a very narrow border to the pygidium. *Dolichometopsis* has a pygidium without a border and with a terminal indentation, and *Glossopleura* has very faint glabellar furrows, only eight thoracic segments, and differs in the position of the palpebral lobes.

Monella perplexa gen. et sp. nov.

(Pl. 11, figs. 15–21)

1919 *Ogygia* sp. (*pars*); Lake *in* Greenly : 446.

DIAGNOSIS. As for genus.

DESCRIPTION. Outline ovate, cephalon larger than pygidium. Cephalon semicircular, over twice as broad as long. Glabella clavate, between one and one-quarter and two times as long as broad, convex transversely and slightly convex longitudinally; glabellar lobes with independent convexity; three pairs of glabellar furrows, one quarter the width of the glabella, shallow at their abaxial ends; posterior pair (1p) at one quarter the length of the glabella forwards, inclined obliquely backwards and becoming shallower and wider at their adaxial ends; 2p inclined slightly backwards, situated just forward of half the length of the glabella; 3p transverse or slightly inclined forwards, nearer 2p than the front of the glabella; anterior margin of glabella convex forwards, lateral margins and the distinct axial furrows evenly and gently convex adaxially, with well marked fossulae midway between 3p and the front of the glabella. Occipital ring continues the convexity of the glabella, one sixth its length (*sag.*); occipital furrow distinct. Fixigenae smaller than the glabella or the librigenae. Palpebral lobes semicircular, posterior extremities just anterior to the base of the glabella; anterior extremities between the 2p and 3p furrows, separated from the axial furrows at each end by one-third the width of the glabella. No preglabellar field. Anterior border furrow narrow, anterior border with a vertically deflected margin. Facial sutures opisthoparian, posterior branches diverging backwards to cut the posterior margin midway between the axial furrow and the genal spine; anterior branches run directly forwards from the eye to the margin. Librigenae convex, genal spine equal in length to the glabella. Posterior border straight to the facial suture, then curving abaxially from it evenly round to the genal spine; posterior and lateral furrows well defined, posterior border half the width of the occipital ring (*sag.*); the lateral border with a vertical deflection. Doublure wide.

Hypostome and rostral plate unknown.

Thorax of eleven segments. Axis cylindrical, tapering slightly, equal in width to the pleural regions, articulating half-rings equal in length (*sag.*) to the axial rings; interpleural furrows curving slightly forwards towards the axial furrows. Pleural regions flat adaxially, deflected ventrally in their abaxial regions; pleural furrows transverse, dying out between fulcra and extremities; short, backwardly directed pleural spines formed by the extremities of the pleurae being tapered.

Anterior three(?) segments narrower (*tr.*) than the rest and undeflected at their ends.

Pygidium semicircular. Axis convex, tapering to a point and extending onto the border but not reaching the posterior margin, eight or possibly more axial rings present. Pleural lobes gently convex with pleural furrows only. Border broad, concave, doublure equal to it in width.

Type specimens (measurements in mm.)

		Length	Width
Holotype.	Counterpart moulds of complete dorsal carapace (Af.827–8)	—	13·7
Paratypes.	Internal mould of cranidium (Af.834) .	—	—
	Internal mould of cranidium (Af.836) .	—	—
	Internal mould of pygidium (Af.839) .	—	—
Other figured specimen			
	External mould of incomplete dorsal carapace (In.58290)	—	—

Type horizon and locality. Carmel Formation, sandstones in old quarry (now filled in), 400 yds. north-north-west of Bryn Gollen Uchaf, Llanerchymedd. N.G.R. 40508425. Other figured specimen from same horizon, on the escarpment 50 yds. north-east of Prys-owain-bach, Carmel. N.G.R. 38878283.

Discussion. The generic position of *M. perplexa* has already been discussed, and it is at present the only species known of the genus.

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PLATE 1

Hesperonomiella carmelensis sp. nov.

Carmel Formation, sandstones 50 yds. north-east of Prys-owain-bach, Carmel.

FIG. 1. Latex cast of ventral interior. BB.30531. ×1·4.
FIG. 2. Latex cast of ventral interior. BB.30530. ×1·5.
FIG. 3. Internal mould of pedicle valve. BB.30532a. ×1·5.
FIG. 4. Holotype, latex cast of dorsal interior. BB.30529. ×1·5.
FIG. 5. Latex cast of ventral exterior. BB.30532b. ×1·6.
FIG. 6. Latex cast of dorsal exterior. BB.30533. ×1·3.

Monorthis typis gen. et sp. nov.

Treiorwerth Formation, sandstone 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIGS. 7, 8. Holotype, internal mould and latex cast of brachial valve. BB.30534. ×3·4.
FIG. 9 Latex cast of dorsal interior. BB.30535a. ×4·7.
FIG. 10. Latex cast of dorsal exterior. BB.30535b. ×3·2.
FIGS. 11, 12. Internal mould and latex cast of pedicle valve. BB.30536a. ×3·2.
FIG. 13. Latex cast of ventral exterior. BB.30536b. ×3·2.

Orthambonites(?) sp. (1)

Nantannog Formation, gritty shales 220 yds. west of Fferam-uchaf, Llanbabo.

FIGS. 14, 17. Latex cast and mould of dorsal interior. Af.1398. ×4·0, ×2·5.
FIG. 16. Latex cast of dorsal exterior. Af.1399. ×4·0.

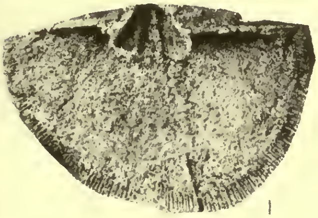
Orthambonites (?) sp. (2)

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 15. Latex cast of ventral interior. BB.30510. ×3·3.
FIGS. 18, 19. Internal mould and latex cast of pedicle valve. BB.30511a. ×2·9.
FIG. 20. Latex cast of ventral exterior. BB.30511b. ×2·9.

Lenorthis proava (Salter)

Carmel Formation, sandstones 50 yds. north-east of Prys-owain-bach, Carmel.
FIG. 21. Internal mould of brachial valve. BB.30512. ×2·3.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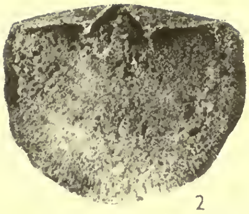
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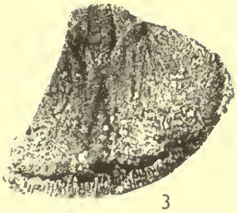
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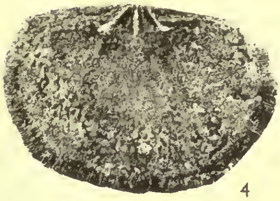
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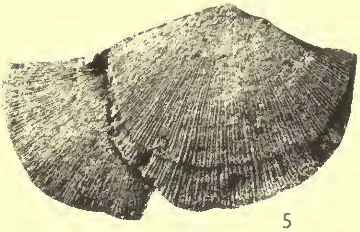
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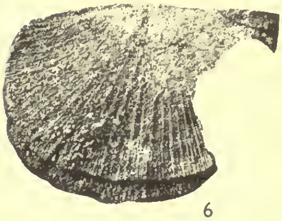
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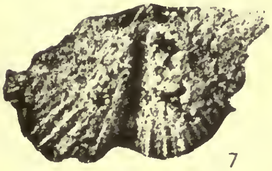
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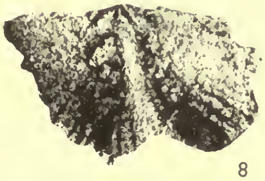
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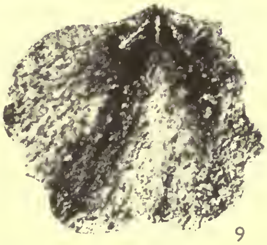
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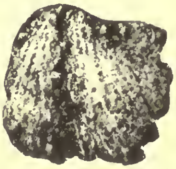
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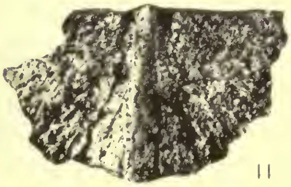
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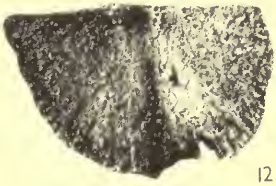
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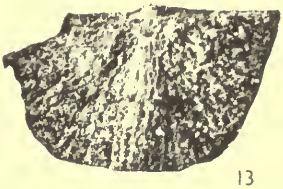
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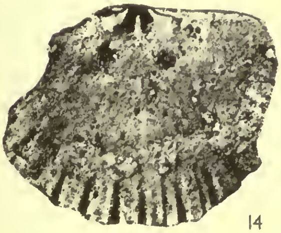
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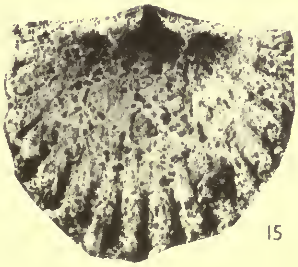
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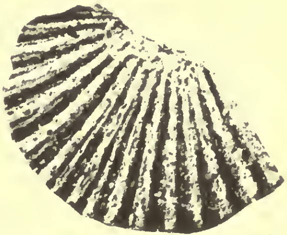
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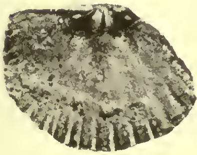
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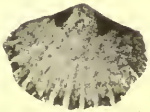
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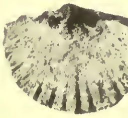
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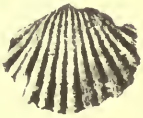
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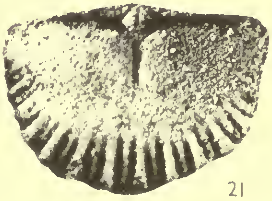
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PLATE 2

Lenorthis proava (Salter)

Carmel Formation, sandstones 50 yds. north-east of Prys-owain-bach, Carmel.

FIG. 1. Latex cast of dorsal interior. BB.30512. ×2·1.
FIG. 2. Latex cast of dorsal interior. BB.30515a. ×2·2.
FIG. 4. Latex cast of dorsal exterior. BB.30515b. ×2·1.
FIG. 5. Latex cast of ventral exterior. BB.30513b. ×2·0.
FIG. 7. Latex cast of ventral interior. BB.30514. ×2·8.
FIG. 8. Latex cast of ventral interior. BB.30513a. ×2·2.

Carmel Formation, sandstones 130 yds. north-west of Ty-hen, Treiorwerth.

FIGS. 3, 6. Internal mould and latex cast of pedicle valve. Af.1337. ×2·4.

Cyrtonotella sp. (1)

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIGS. 9, 13. Internal mould and latex cast of brachial valve. BB.30521a. ×5·0.
FIG. 10. Latex cast of dorsal exterior. BB.30521b. ×5·0.

Lenorthis sp.

Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach cottage, Bod Deiniol.

FIG. 11. Latex cast of dorsal interior. BB.30602. ×2·1.
FIG. 12. Latex cast of ventral interior. BB.30601a. ×2·7.

Cyrtonotella sp. (2)

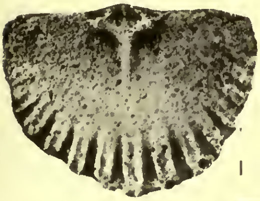
Garn Formation, limestone blocks in breccia beds, Porth-Padrig, Mynachdy.

FIG. 14. Exterior of brachial valve. BB.30523. ×2·4.
FIG. 15. Latex cast of dorsal exterior. BB.30524. ×2·3.
FIG. 16. Exterior of pedicle valve. BB.30522. ×3·2.

Pleurorthis costatus sp. nov.

Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIGS. 17, 18. Holotype, internal mould and latex cast of brachial valve. BB.30516. ×2·2.
FIG. 19. Latex cast of dorsal exterior. BB.30555b. ×3·3.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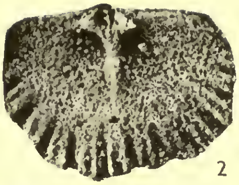
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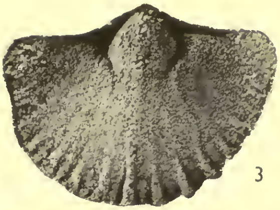
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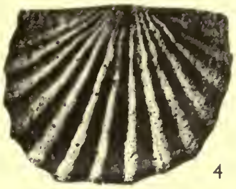
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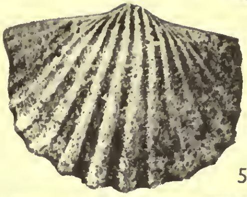
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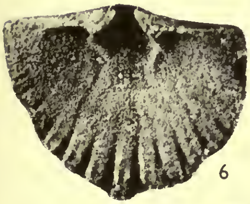
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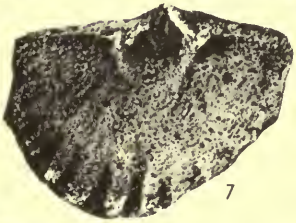
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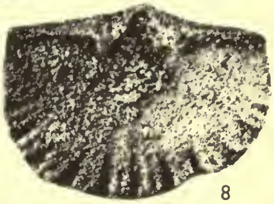
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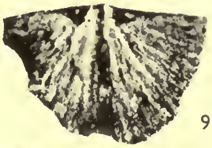
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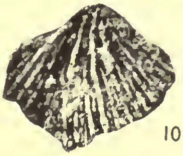
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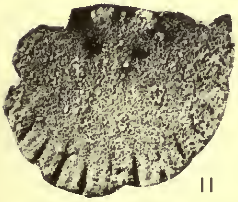
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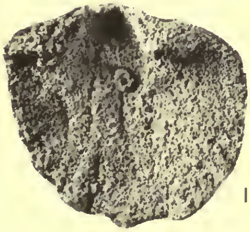
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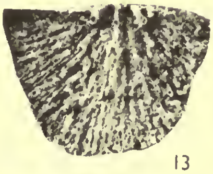
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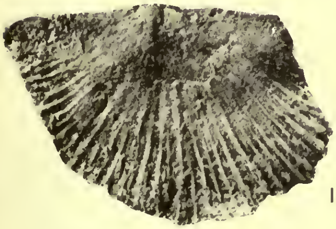
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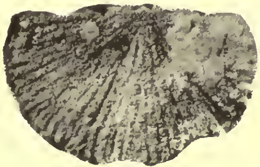
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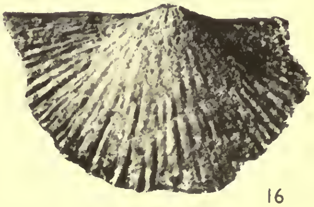
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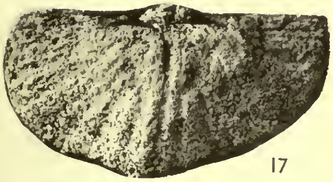
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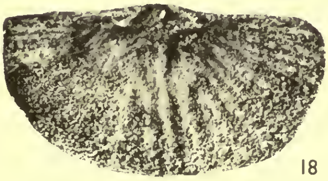
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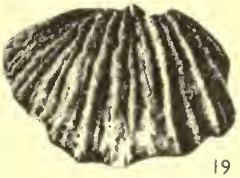
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PLATE 3

Pleurorthis costatus sp. nov.

Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIGS. 1, 2. Internal mould and latex cast of pedicle valve. BB.30518. ×2·2.
FIGS. 3, 4. Internal mould and latex cast of pedicle valve. BB.30517a. ×2·3.
FIG. 6. Latex cast of ventral exterior. BB.30517b. ×2·3.

Nicolella humilis Williams

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 5. Latex cast of dorsal interior. BB.30519a. ×3·1.
FIG. 7. Latex cast of dorsal exterior. BB.30519b. ×3·1.
FIG. 8. Latex cast of dorsal exterior. BB.30520b. ×3·3.
FIG. 9. Internal mould of brachial valve. BB.30520a. ×3·1.

Panderina lamellosa sp. nov.

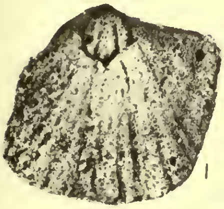
Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIG. 10. Latex cast of dorsal interior. BB.30528a. ×4·2.
FIGS. 11, 12. Holotype, internal mould and latex cast of brachial valve. BB.30525a. ×4·2.
FIG. 13. Latex cast of dorsal exterior. BB.30528b. ×3·0.
FIG. 14. Holotype, latex cast of dorsal exterior. BB.30525b. ×4·0.
FIGS. 15, 16. Latex cast and internal mould of pedicle valve. BB.30526a. ×5·5.
FIG. 17. Latex cast of ventral exterior. BB.30527b. ×3·2.
FIG. 18. Latex cast of ventral interior. BB.30527a. ×4·3.

Ptychopleurella sp. (1)

Nantannog Formation, fine sandstones and shales 190 yds. south-east of Fferam-uchaf farm, Llanbabo.

FIG. 19. Latex cast of ventral interior. BB.30537a. ×4·1.
FIG. 20. External mould of pedicle valve. BB.30537b. ×4·6.
FIGS. 21, 22. Internal mould and latex cast of brachial valve. BB.30538a. ×4·5.
FIG. 23. Latex cast of dorsal exterior. BB.30538b. ×4·5.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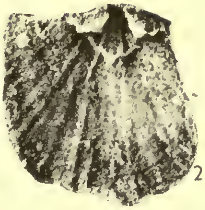
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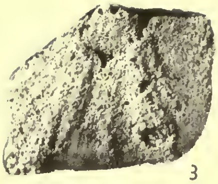
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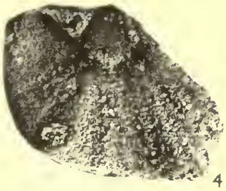
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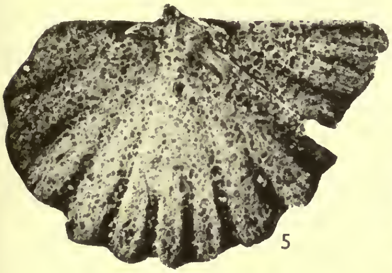
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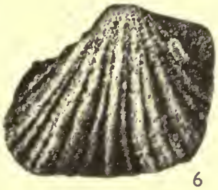
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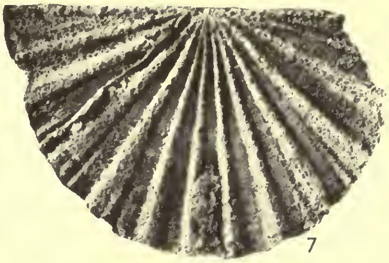
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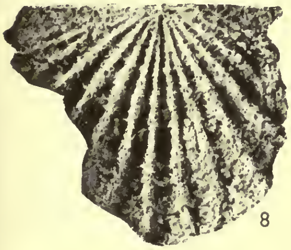
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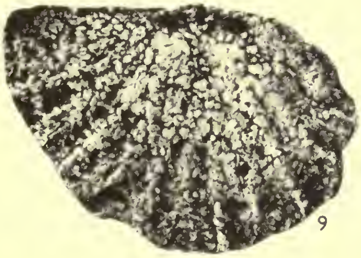
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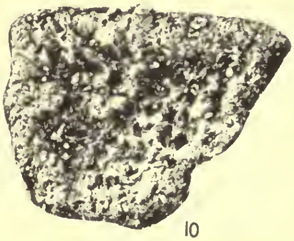
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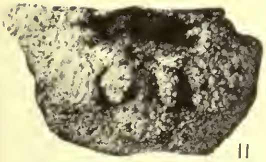
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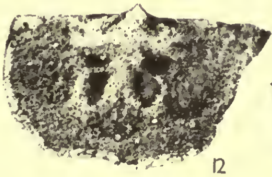
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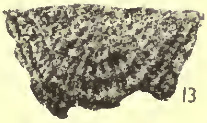
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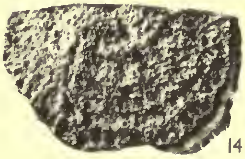
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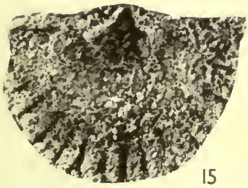
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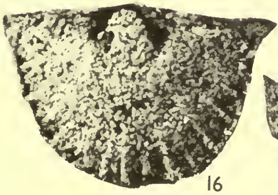
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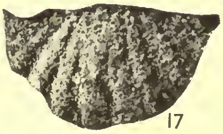
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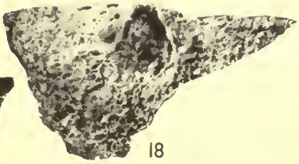
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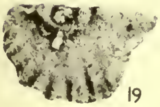
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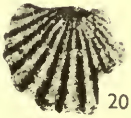
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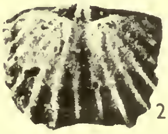
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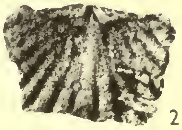
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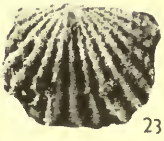
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PLATE 4

Ptychopleurella sp. (2)

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 1. Internal mould of brachial valve. BB.30539a. ×3·5.
FIGS. 2, 3. Internal mould and latex cast of pedicle valve. BB.30540a. ×4·1.
FIG. 5. Fragment of external mould of pedicle valve. BB.30540b. ×4·0.

Dolerorthis cf. ***tenuicostata*** Williams

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 4. Latex cast of ventral exterior. BB.30541b. ×3·1.
FIGS. 6, 7. Internal mould latex cast of pedicle valve. BB.30541a. ×2·6, ×3·1.

Plaesiomys cf. ***robusta*** (Bancroft)

Crewyn Formation, grits 420 yds. west-south-west of Ysgubor-gader, Mynachdy.

FIG. 8. Latex cast of dorsal exterior. BB.30543b. ×2·0.
FIG. 9. Latex cast of dorsal interior. BB.30543a. ×2·2.
FIG. 10. Internal mould of pedicle valve. BB.30544a. ×1·7.
FIG. 11. External mould of pedicle valve. BB.30545b. ×1·7.
FIG. 12. Internal mould of pedicle valve. BB.30545a. ×1·7.

Plaesiomys **(*Dinorthis*)** sp.

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIGS. 13, 15. Internal mould and latex cast of pedicle valve. BB.30542a. ×2·6.
FIG. 14. Latex cast of ventral exterior. BB.30542b. ×3·2.

Plectorthis (?) sp.

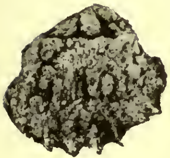
Nantannog Formation, gritty shales 250 yds. west-south-west of Fferam-uchaf, Llanbabo.

FIG. 16. Internal mould of pedicle valve. Af.1377. ×4·0.
FIG. 19. Internal mould of pedicle valve. Af.1462. ×2·9.

Platystrophia precedens major Williams

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 17. Latex cast of ventral interior. BB.30546a. ×2·2.
FIG. 18. Latex cast of ventral exterior. BB.30546b. ×2·0.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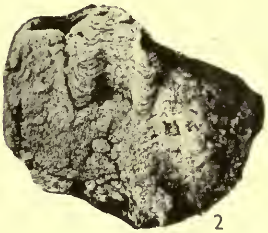
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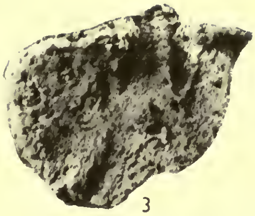
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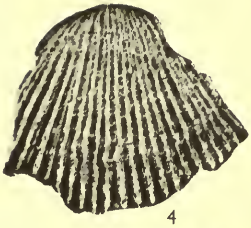
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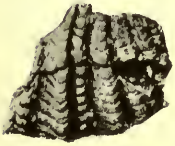
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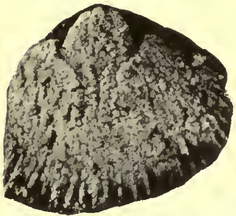
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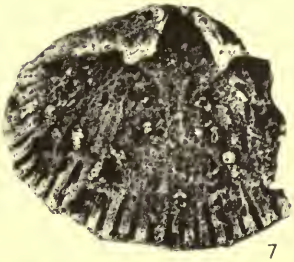
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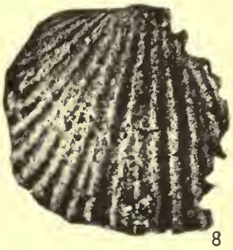
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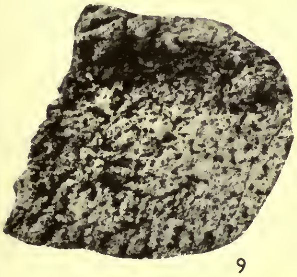
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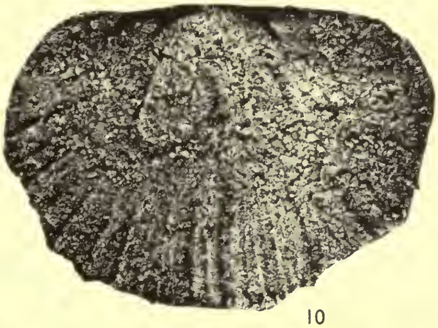
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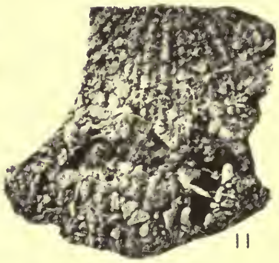
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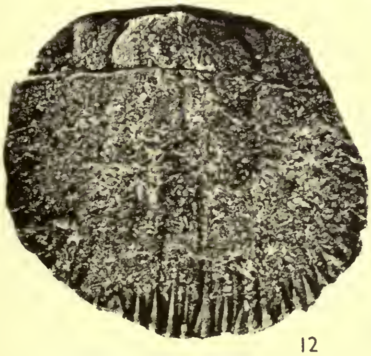
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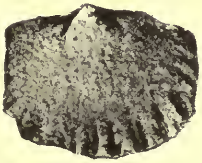
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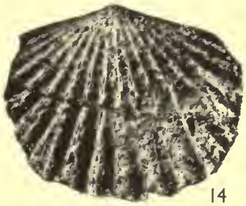
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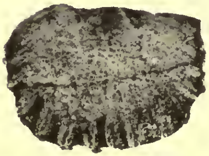
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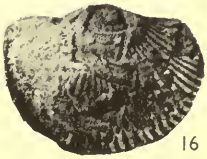
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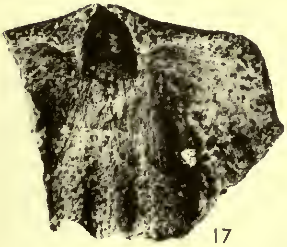
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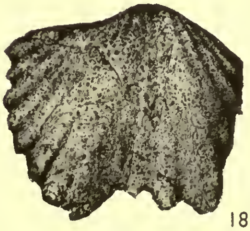
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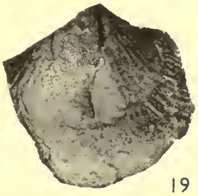
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PLATE 5

Skenidioides sp. (1)

Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIG. 1. Internal mould of pedicle valve. BB.30547. ×7·7.
FIG. 2. Internal mould of brachial valve. BB.30548. ×6·1.

Skenidioides sp. (2)

Nantannog Formation, fine sandstones and shales 190 yds. south-east of Fferam-uchaf, Llanbabo.

FIG. 3. Internal mould of brachial valve. BB.30549a. ×6·5.
FIG. 4. Internal mould of pedicle valve. BB.30550a. ×7·6.
FIG. 5. External mould of brachial valve. BB.30549b. ×6·5.

Paurorthis(?) sp.

Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach cottage, Bod Deiniol.

FIGS. 6, 7. Internal mould and latex cast of pedicle valve. BB.30603a. ×2·5.
FIG. 8. Latex cast of ventral interior. BB.30604a. ×2·5.
FIG. 9. Latex cast of ventral exterior. BB.30604b. ×2·5.

Dalmanella(?) sp.

Crewyn Formation, grits 420 yds. west-south-west of Ysgubor-gader, Mynachdy.

FIG. 10. Latex cast of brachial exterior. BB.30568. ×2·5.
FIG. 11. Latex cast of ventral exterior. BB.30569. ×2·7.

Onniella(?) sp.

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 12. Internal mould of pedicle valve. BB.30570a. ×3·7.
FIG. 13. Latex cast of ventral exterior. BB.30570b. ×3·9.
FIG. 14. Internal mould of brachial valve. BB.30571. ×4·9.

Horderleyella(?) sp.

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 15. Internal mould of pedicle valve. BB.30572. ×2·9.

Harknessella sp.

Garn Formation, limestone block in breccia bed, 300 yds. east-south-east of the summit of Mynydd-y-garn.

FIG. 16. Exterior of pedicle valve. Af.1492. ×3·0.

Salopia salteri gracilis Williams

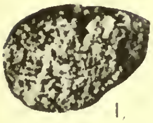
Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIGS. 17, 18. Internal mould and latex cast of brachial valve. BB.30573. ×3·9, ×4·1.

Rhynchorthis rotundus gen. et sp. nov.

Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIGS. 19, 20. Holotype, internal mould and latex cast of brachial valve. BB.30551. ×2·9, ×3·5.
FIGS. 21, 22. Internal mould and latex cast of brachial valve. BB.30552. ×3·4, ×3·7.
FIGS. 23, 25. Internal mould and latex cast of pedicle valve. BB.30556. ×3·4, ×3·1.
FIG. 24. Internal mould of pedicle valve. BB.30554. ×3·2.
FIG. 26. Internal mould of brachial valve. BB.30553. ×3·0.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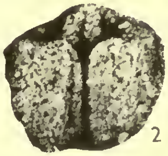
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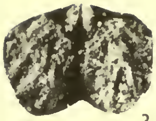
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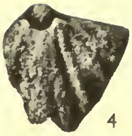
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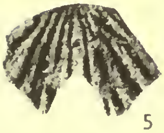
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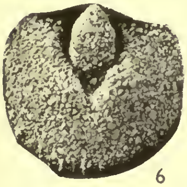
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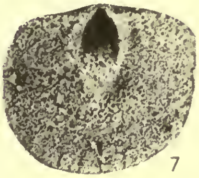
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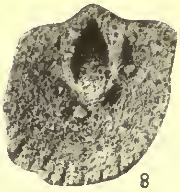
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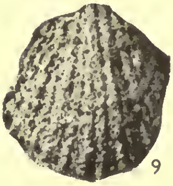
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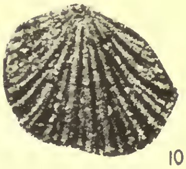
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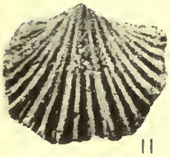
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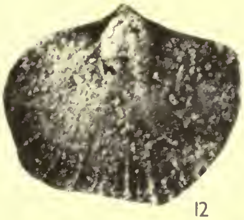
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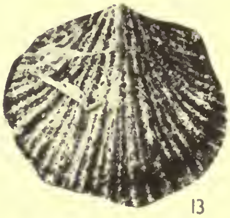
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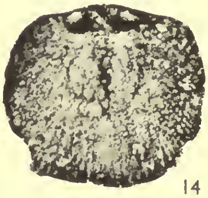
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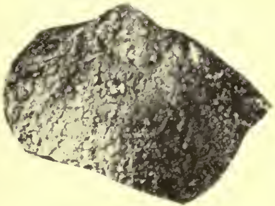
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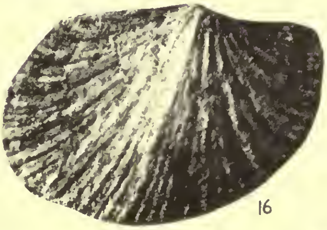
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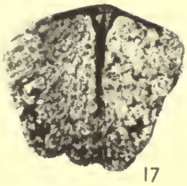
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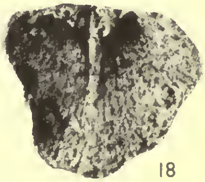
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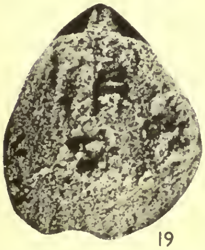
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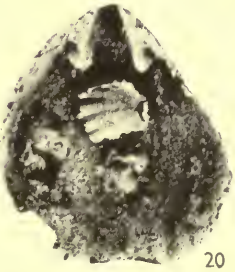
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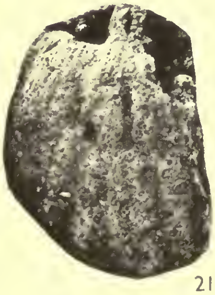
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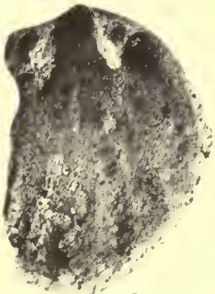
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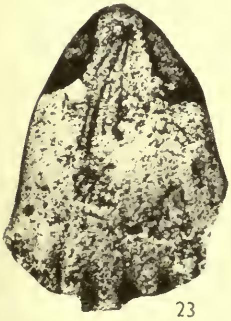
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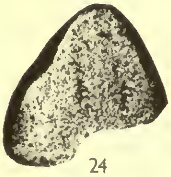
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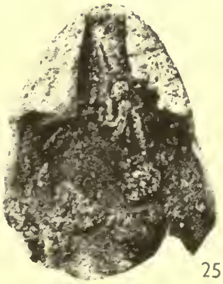
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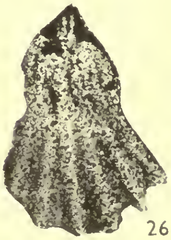
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PLATE 6

Tritoechia sp.

Treiorwerth Formation, sandstones 300 yds south-east of Ffynnon-y-mab, Trefor.

FIG. 1. Latex cast of ventral interior. BB.30557a. ×2·2.

FIG. 2. Latex cast of ventral interior, and exterior of interarea, posterior view. BB.30557a. ×2·2.

FIGS. 3, 5. Latex cast of ventral exterior, posterior and ventral views. BB.30557b. × 2·0.

Clitambonites(?) sp.

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 4. Latex cast of dorsal exterior. BB.30558. ×1·4.

Ilmarinia sp.

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIGS. 6, 7. Internal mould of pedicle valve, ventral and posterior views. BB.30559a. ×3·1.

Apomatella(?) sp.

Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach cottage, Bod Deiniol.

FIG. 8. Latex cast of ventral interior. BB.30605a. ×3·0.
FIG. 9. Latex cast of ventral exterior, posterior view. BB.30605b. ×3·0.
FIG. 10. Latex cast of ventral exterior, posterior view. BB.30606b. ×2·3.
FIG. 11. Latex cast of ventral interior. BB.30606a. ×2·4.

Antigonambonites pyramidalis sp. nov.

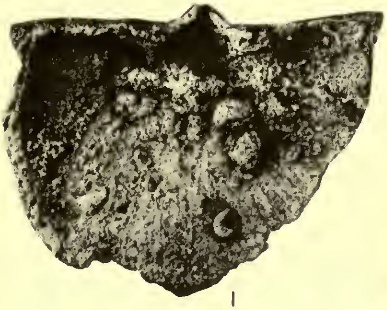
Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIG. 12. Holotype, latex cast of dorsal interior. BB.30561a. ×4·1.
FIG. 13. Holotype, latex cast of dorsal exterior. BB.30561b. ×4·4.
FIGS. 14, 15. Latex cast and internal mould of brachial valve. BB.30563. ×2·8, ×2·2.
FIGS. 16, 17. Internal mould and latex cast of pedicle valve. BB.30564. ×3·3, ×3·5.
FIG. 18. Internal mould of pedicle valve. BB.30562. ×4·0.

Kullervo aff. ***panderi*** (Öpik)

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIGS. 19, 20. Internal mould and latex cast of brachial valve. BB.30567a. ×4·0.
FIG. 21. Latex cast of dorsal exterior. BB.30567b. ×4·0.
FIG. 22. Internal mould of pedicle valve. BB.30565. ×2·5.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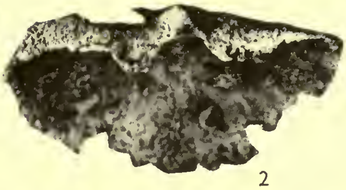
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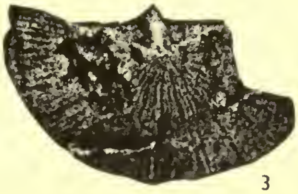
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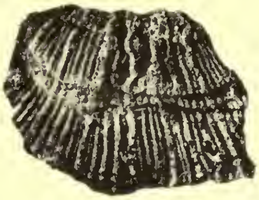
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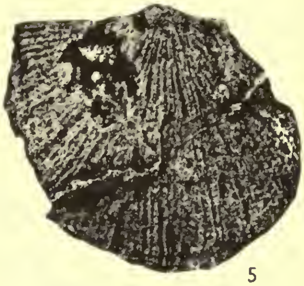
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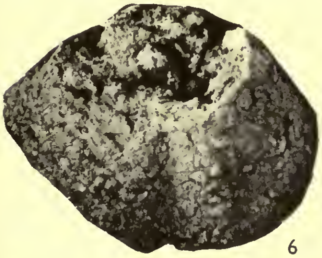
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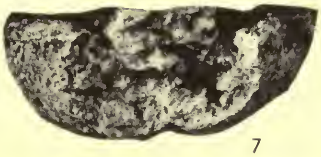
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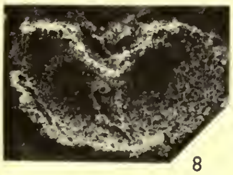
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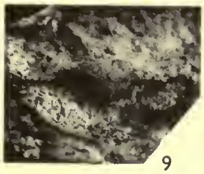
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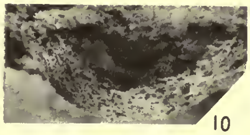
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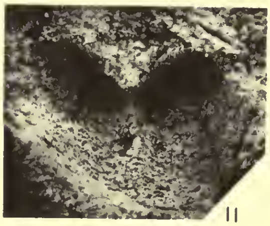
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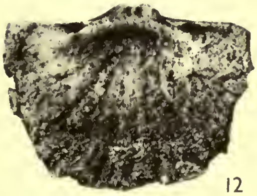
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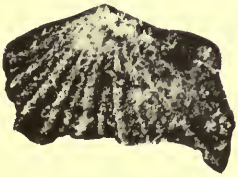
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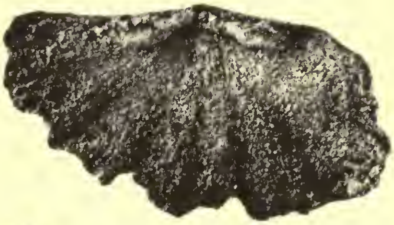
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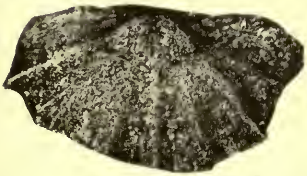
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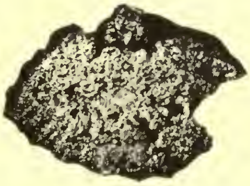
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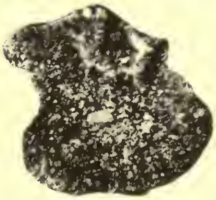
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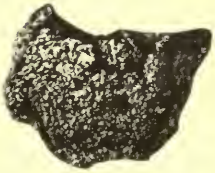
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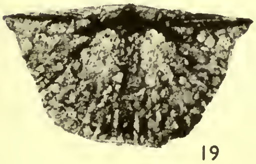
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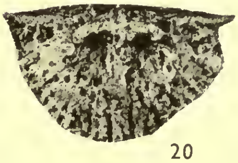
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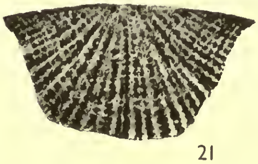
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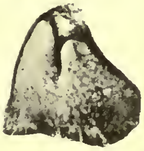
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PLATE 7

Kullervo aff. ***panderi*** (Öpik)

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 1. Latex cast of ventral interior. BB.30566. ×5·1.

Estlandia(?) sp.

Berw-uchaf Grits, 90 yds. north of Bwlch-gwyn farm, Holland Arms.

FIG. 2. Latex cast of ventral interior. Af.238. ×5·2.
FIG. 3. Latex cast of ventral exterior. Af.225. ×5·2.
FIGS. 4, 9. Internal mould and latex cast of brachial valve. Af.214. ×5·0.
FIGS. 6, 7. Internal mould and latex cast of brachial valve. BB.30560a. ×7·7.
FIG. 8. Latex cast of dorsal exterior. BB.30560b. ×7·7.

Clitambonitid gen. indet.

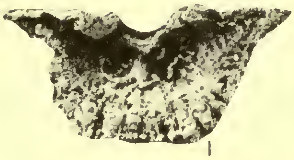
Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach cottage, Bod Deiniol.

FIG. 5. Latex cast of dorsal interior. BB.30608a. ×2·0.
FIGS. 10, 11. Latex cast of ventral interior, dorsal and anterior views. BB.30607. ×3·0.

Ahtiella concava sp. nov.

Bod Deiniol Formation, grits in temporary excavation 50 yds. north of Ty-bach cottage, Bod Deiniol.

FIG. 13. Latex cast of dorsal interior. BB.30616a. ×2·4.
FIG. 12. Latex cast of dorsal interior, cardinalia. BB.30616a. ×3·0.
FIG. 14. Holotype, latex cast of ventral interior. BB.30615a. ×1·9.
FIGS. 15, 18. Holotype, latex cast of ventral exterior, ventral and posterior views. BB. 30615b. ×1·9.
FIGS. 16, 19. Latex cast of dorsal interior, ventral and oblique posterior views. BB. 30618a. ×2·4.
FIG. 22. Latex cast of dorsal exterior. BB.30616b. ×2·3.
FIG. 17. Latex cast of dorsal interior. BB.30617a. ×2·2.
FIG. 20. Latex cast of ventral interior. BB.30619a. ×2·3.
FIG. 21. Latex cast of ventral exterior. BB.30619b. ×2·2.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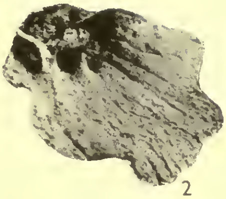
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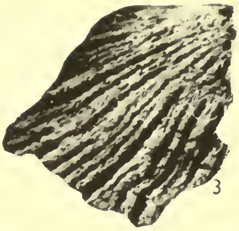
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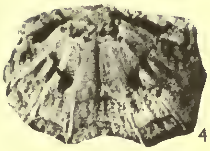
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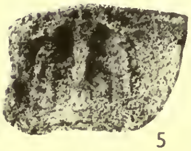
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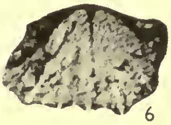
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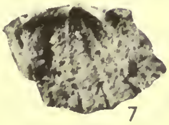
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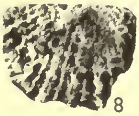
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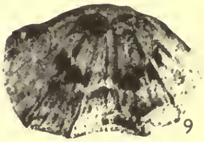
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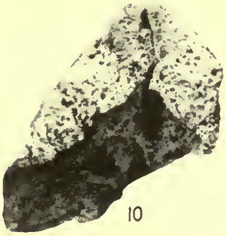
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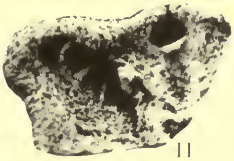
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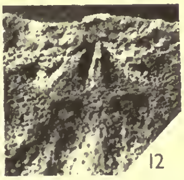
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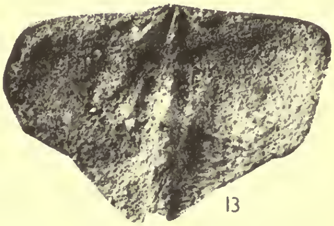
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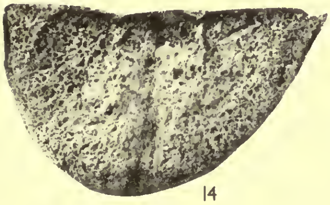
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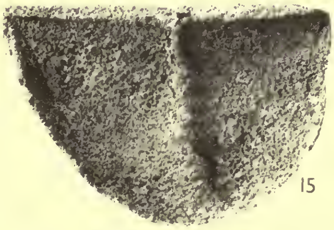
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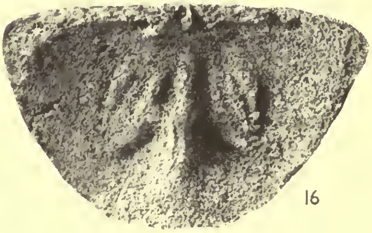
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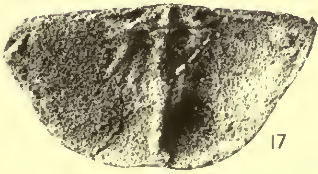
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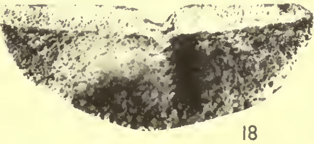
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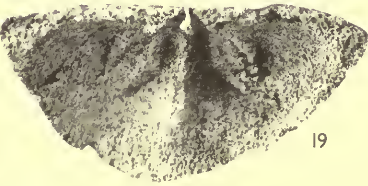
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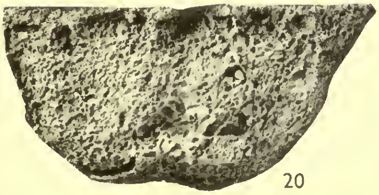
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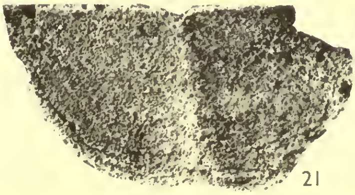
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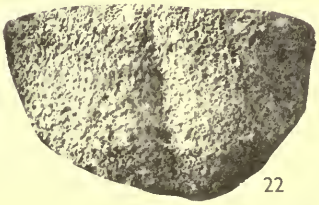
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PLATE 8

Ahtiella quadrata sp. nov.

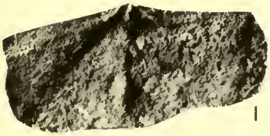
Torllwyn Formation, sandstones 50 ft. above the base of the succession, on the north side of the faulted syncline, 45 yds. north of Ogof Gynfor, Llanbadrig.

Fig. 1. Latex cast of dorsal interior. BB.30613a. ×2·2.
Fig. 4. Latex cast of dorsal exterior. BB.30613b. ×2·0.
Fig. 2. Latex cast of ventral interior. BB.30611a. ×2·0.
Fig. 3. Latex cast of ventral exterior. BB.30611b. ×2·0.
Fig. 5. Latex cast of dorsal interior. BB.30612a. ×2·2.
Fig. 6. Latex cast of dorsal exterior. BB.30612b. ×1·9.
Fig. 7. Latex cast of dorsal interior. BB.30614a. ×2·3.
Fig. 8. Holotype, latex cast of ventral interior. BB.30609. ×2·0.
Fig. 9. Latex cast of ventral interior. BB.30610. ×2·0.

Reinversella monensis gen. et sp. nov.

Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

Figs. 10, 11. Holotype, internal mould and latex cast of brachial valve. BB.30574a. ×1·6.
Fig. 12. Holotype latex cast of dorsal exterior. BB.30574b. ×1·6.
Figs. 13, 14. Internal mould and latex cast of pedicle valve. BB.30575a. ×1·9, ×1·7.
Fig. 15. Latex cast of ventral exterior. BB.30575b. ×2·2.
Fig. 16. Internal mould of brachial valve. BB.30576a. ×2·1.
Fig. 17. Latex cast of dorsal exterior. BB.30576b. ×2·2.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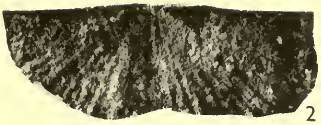
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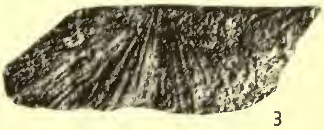
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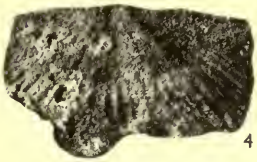
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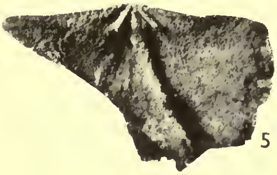
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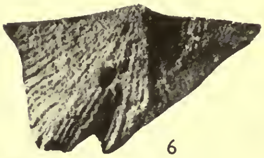
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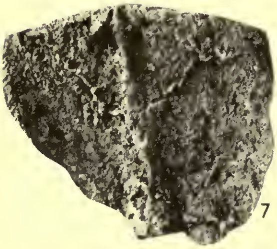
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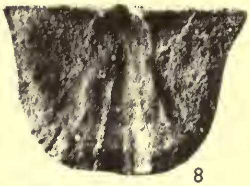
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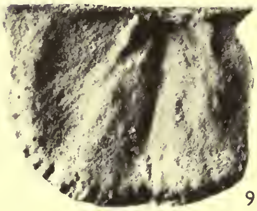
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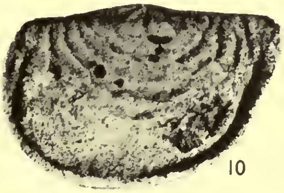
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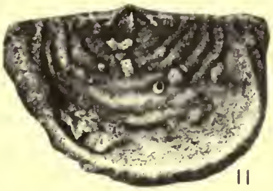
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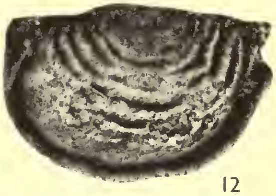
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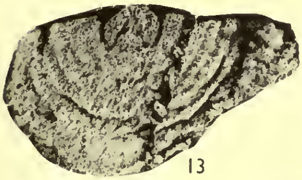
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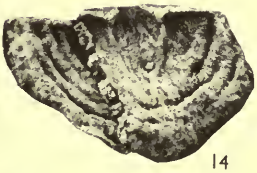
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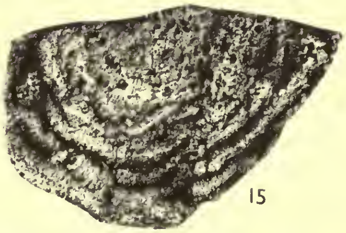
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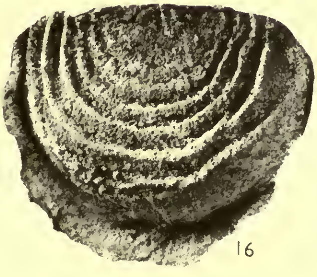
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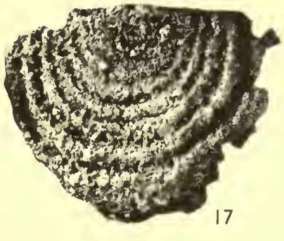
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PLATE 9

Palaeostrophomena(?) sp.

Garn Formation, limestone blocks in breccia beds at Porth Padrig, Mynachdy.

FIG. 1. Exterior of pedicle(?) valve. BB.30581a. ×2·2.

Sericoidea abdita Williams

Tandinas Shales, by the shore 100 yds. west of the pier, Careg-onen.

FIG. 3. Internal mould of brachial valve with shell material adhering. BB.30588. ×7·1.
FIG. 6. Interior of brachial valve. BB.30587. ×7·3.

Palaeostrophomena sp.

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIG. 2. Latex cast of ventral interior. BB.30579a. ×3·2.
FIGS. 4, 5. Internal mould and latex cast of brachial valve. BB.30580. ×3·0.

Leptestiina derfelensis (Jones)

Tandinas Shales, by the track 50 yds. west of Tandinas Quarry, Careg-onen.

FIGS. 7, 8. Internal mould and latex cast of pedicle valve. BB.30577. ×4·0.
FIG. 9. Latex cast of dorsal interior. BB.30578. ×4·4.

Bilobia aff. ***musca*** (Öpik)

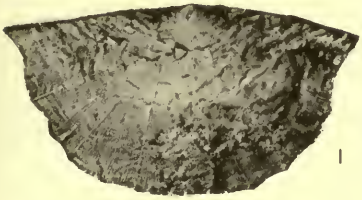
Llanbabo Formation, Llanbabo Church Grits, 180 yds. east of Fferam-uchaf, Llanbabo.

FIGS. 10, 11. Internal mould of pedicle valve, ventral and posterior views. BB.30582. ×3·0, ×4·0.
FIG. 12. Latex cast of ventral interior. BB.30582. ×3·0.
FIG. 13. Internal mould of part of brachial valve. BB.30583. ×3·3.

Eoplectodonta lenis Williams

Llanbabo Formation, Llanbabo Church Grits, Church Quarry, Llanbabo.

FIGS. 14, 15. Internal mould and latex cast of pedicle valve. BB.30584a. ×4·0, ×3·7.
FIG. 16. Internal mould of brachial valve. BB.30585a. ×4·1.
FIG. 17. Latex cast of dorsal exterior. BB.30585b. ×4·1.
FIG. 18. Latex cast of dorsal exterior. BB.30586. ×4·5.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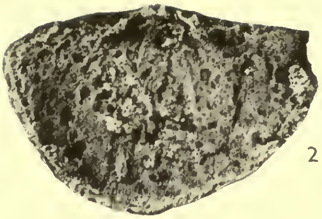
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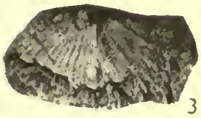
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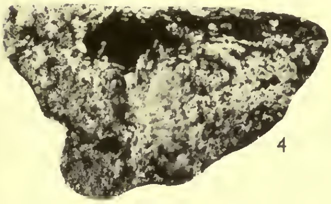
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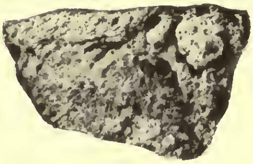
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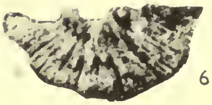
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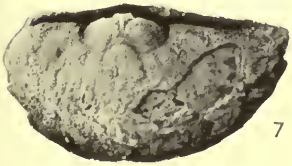
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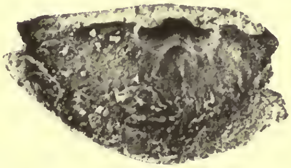
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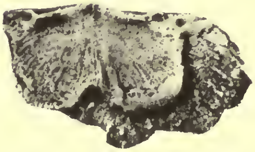
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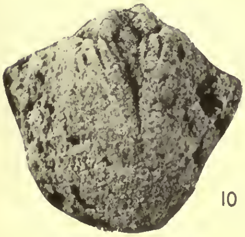
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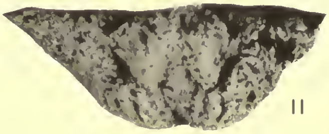
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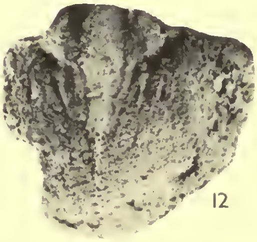
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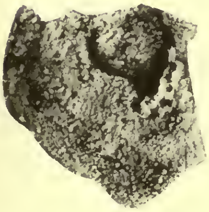
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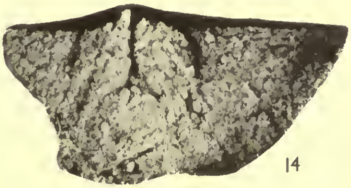
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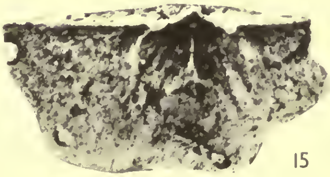
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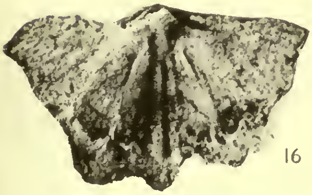
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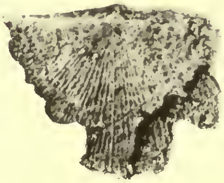
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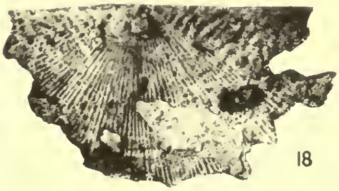
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PLATE 10

Ptychoglyptus sp.

Garn Formation, limestone blocks in breccia beds at Porth Padrig, Mynachdy.

FIG. 1. Exterior of brachial valve. BB.30589. ×4·4.
FIG. 2. Exterior of pedicle valve. BB.30590. ×4·4.

Leptaena sp.

Llanbabo Formation, Llanbabo Church Grits, 180 yds. east of Fferam-uchaf, Llanbabo.

FIG. 3. Latex cast of dorsal interior. BB.30592. ×3·2.
FIGS. 4, 5. Internal mould and latex cast of pedicle valve. BB.30591. ×2·2.
FIG. 6. Internal mould of brachial valve. BB.30593. ×4·5.

Dactylogonia sp.

Nantannog Formation, fine sandstones and shales 190 yds. south-east of Fferam-uchaf farm, Llanbabo.

FIGS. 7, 8. Latex cast and internal mould of brachial valve. BB.30596a. ×5·6, ×4·6.

Kiaeromena(?) sp.

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIG. 9. Exterior of brachial(?) valve. BB.30595. ×2·9.
FIG. 10. Exterior of pedicle(?) valve. BB.30594. ×3·1.

Rectotrophia globularis gen. et sp. nov.

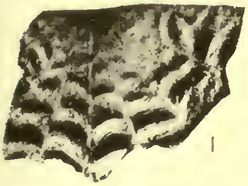
Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

FIGS. 11, 12. Internal mould of brachial valve, dorsal and lateral views. Af.1436. ×3·6.
FIG. 13. Latex cast of internal mould of brachial valve. Af.1436. ×4·7.
FIGS. 14, 15. Holotype, internal mould of pedicle valve, ventral and lateral views. Af.1436. ×3·1.
FIG. 16. Holotype, latex cast of ventral interior. Af.1436. ×4·1.
FIG. 17. Internal mould of brachial valve. Af.1442. ×4·3.

Order uncertain

Torllwyn Formation, sandstones 50 ft. above the base of the succession, on the north side of the faulted syncline, 45 yds. north of Ogof Gynfor, Llanbadrig.

FIGS. 18, 19. Internal mould of brachial valve, posterior and dorsal views. BB.55791a. ×1·5.
FIG. 21. Latex cast of brachial valve. BB.55791a. ×2·2.
FIGS. 20, 22. Internal mould and latex cast of pedicle valve. BB.55792a. ×1·8.
FIG. 23. Latex cast of dorsal exterior. BB.55791b. ×2·1.
FIG. 24. Latex cast of ventral exterior. BB.55792b. ×1·5.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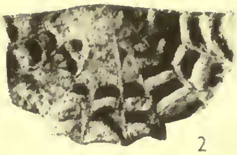
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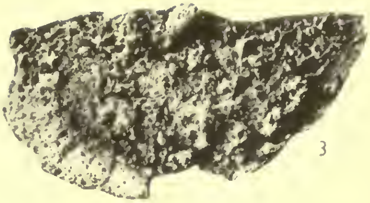
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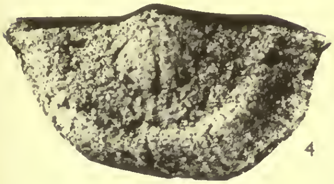
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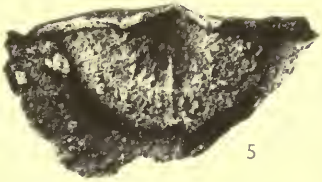
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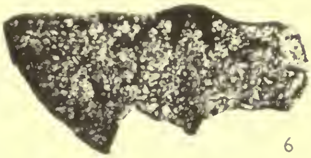
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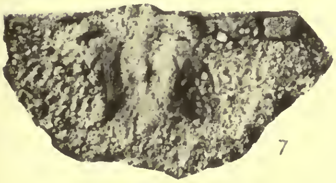
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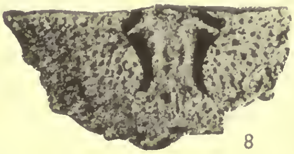
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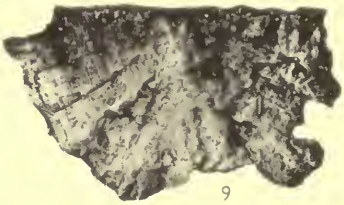
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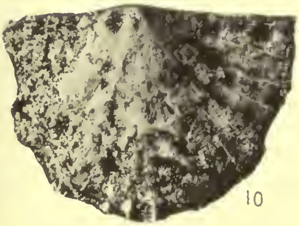
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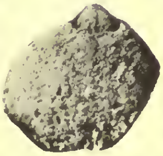
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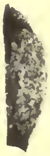
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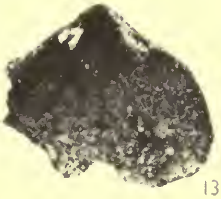
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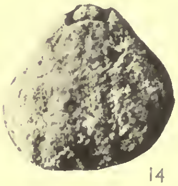
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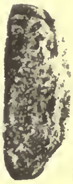
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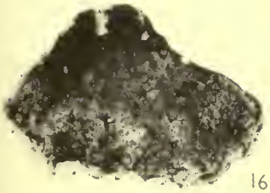
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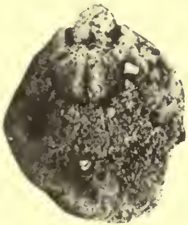
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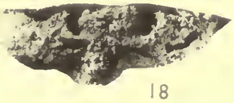
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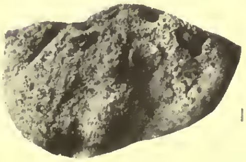
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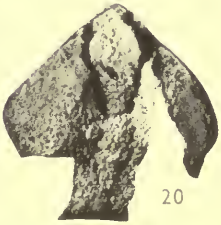
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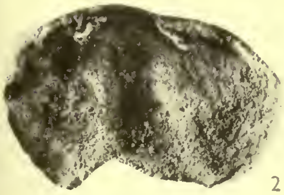
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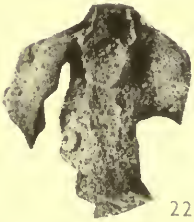
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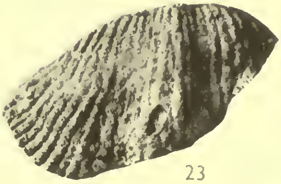
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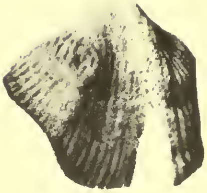
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PLATE 11

Porambonites (s.s.) sp.

Treiorwerth Formation, sandstones 300 yds. south-east of Ffynnon-y-mab, Trefor.

Figs. 1, 2. Internal mould and latex cast of pedicle valve. BB.30598a. ×1·7.
Fig. 3. Internal mould of brachial valve. BB.30599a. ×1·5.
Figs. 4, 8. Latex cast of dorsal interior, dorsal and anterior views. BB.30599a. ×1·3.
Figs. 5, 6. Latex cast and internal mould of brachial valve. BB.30600. ×2·4, ×2·2.

Camerella sp.

Garn Formation, limestone blocks in breccia beds at Porth Padrig, Mynachdy.

Figs. 7, 9, 10, 11. Complete shell, anterior ,dorsal, lateral and ventral views. BB.30597. ×4·8.

Metacamerella cf. ***balcletchiensis*** (Davidson)

Garn Formation, limestone blocks in breccia beds at Porth Padrig, Mynachdy.

Figs. 12, 13, 14. Complete shell, dorsal, lateral and anterior views. Af.1590. ×1·5, ×1·5, ×2·0.

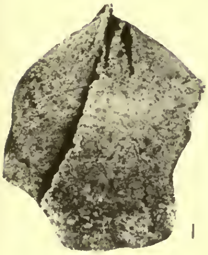
Monella perplexa gen. et sp. nov.

Carmel Formation, sandstone 400 yds. north of Bryn Gollen Uchaf, Llanerchymedd.

Figs. 16, 19. Holotype, internal mould of entire exoskeleton, dorsal and anterior views. Af.827. ×3·0.
Fig. 15. Internal mould of cranidium. Af.836. ×2·4.
Fig. 17. Internal mould of cranidium. Af.834. ×2·5.
Fig. 20. Internal mould of pygidium. Af.839. ×3·1.

Carmel Formation, sandstones 50 yds. north-east of Prys-owain-bach, Carmel.

Figs. 18, 21. Latex casts of external mould of cranidium and one librigena, and incomplete thorax and pygidium. In.58290. ×1·0.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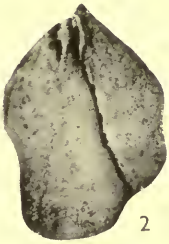
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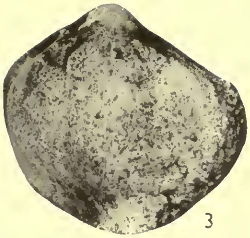
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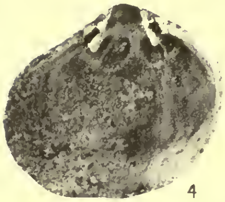
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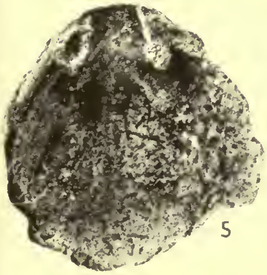
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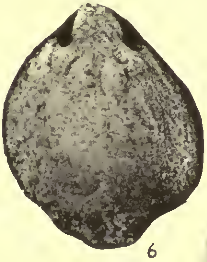
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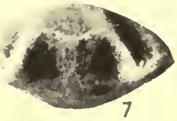
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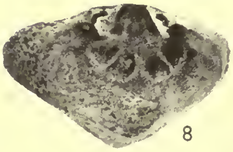
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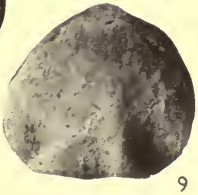
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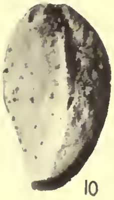
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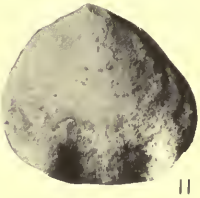
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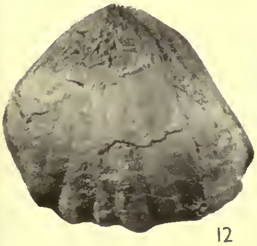
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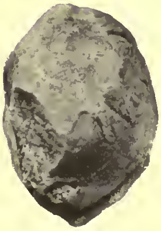
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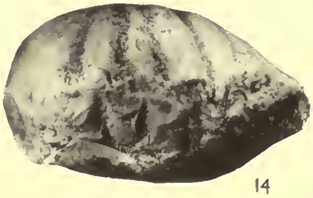
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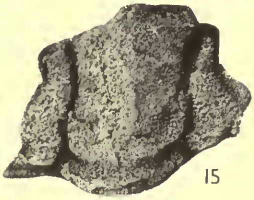
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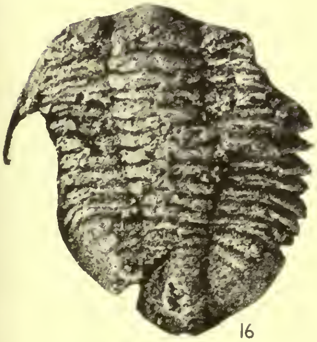
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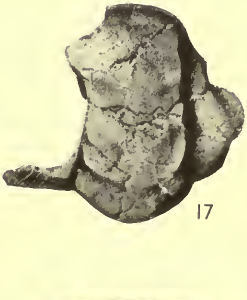
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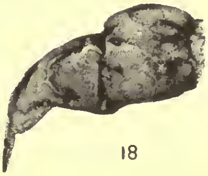
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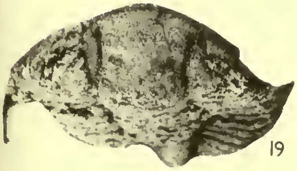
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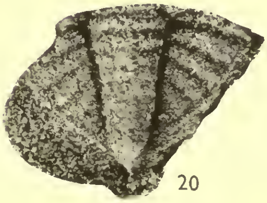
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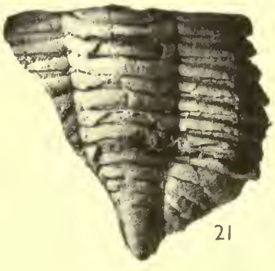
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PLATE 12

Ogygiocaris selwynii (Salter)

Carmel Formation, sandstones 400 yds. north of Bryn Gollen Uchaf, Llanerchymedd.

FIG. 1. Internal mould of cranidium. Af.823. ×1·1.
FIG. 2. Internal mould of cranidium. Af.842. ×1·0.
FIG. 5. Internal mould of pygidium. Af.820. ×1·0.
FIG. 6. Internal mould of pygidium. Af.821. ×1·0.

Protobronteus greenlyi sp. nov.

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIG. 3. Incomplete cranidium. In.58292. ×2·3.
FIG. 4. Internal mould of librigena. In.58293a. ×1·1.
FIG. 7. Holotype, incomplete cranidium. In.58291. ×1·0.

Illaenus sp.

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIGS. 8, 11, 15. Internal mould of cranidium, anterior, dorsal and oblique views. In.58294. ×2·7.

FIGS. 9, 10. Internal mould of pygidium, with doublure partially revealed, lateral and dorsal views. In.58295. ×1·4.

FIGS. 12, 13. Internal mould of pygidium, with some skeletal material adhering, dorsal and lateral views. In.58296. ×1·1.

Stenopareia cf. ***linnarssoni*** (Holm)

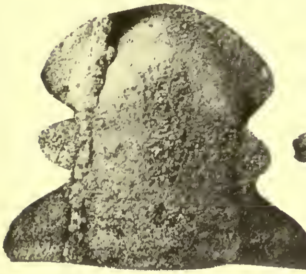
Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIG. 14. Rostral plate. In.58300. ×2·2.
FIG. 16. Internal mould of librigena. In.58299. ×2·0.
FIG. 17. Internal mould of pygidium, showing the doublure. In.58302. ×2·2.

FIGS. 18, 19. Internal mould of incomplete pygidium, with skeletal material adhering, dorsal and lateral views. In.58301. ×1·1.

FIGS. 20, 21. Internal mould of cranidium, anterior and dorsal views. In.58297. ×2·1, ×3·0.

FIGS. 22, 23. Internal mould of cranidium, with some skeletal material adhering, anterior and dorsal views. In.58298. ×2·1.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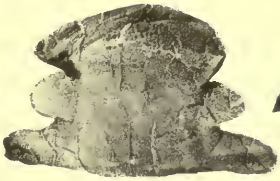
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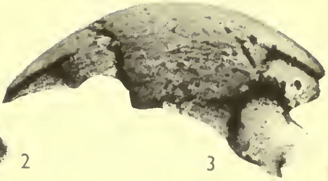
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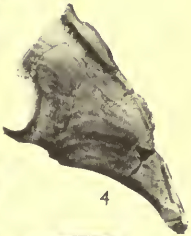
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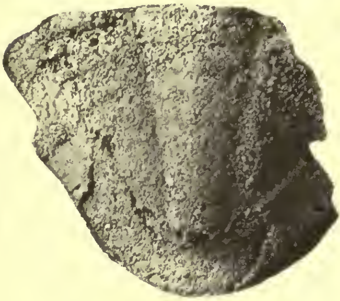
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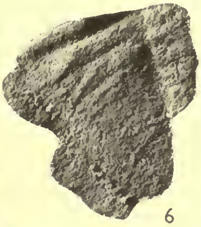
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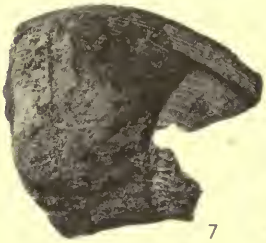
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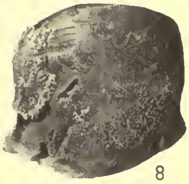
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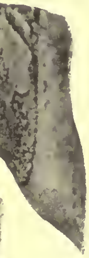
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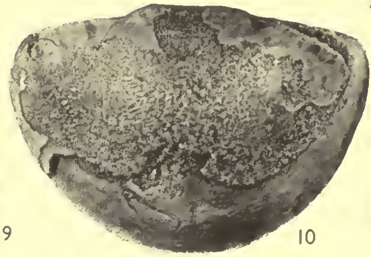
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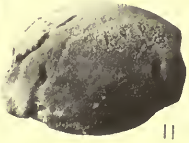
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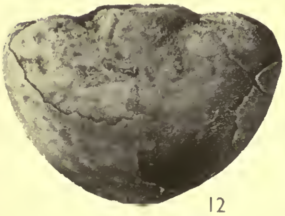
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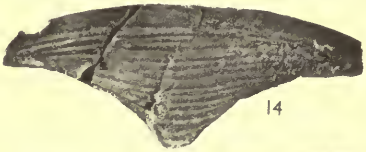
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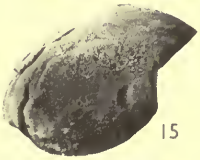
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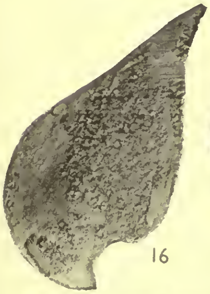
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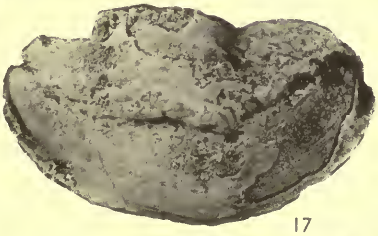
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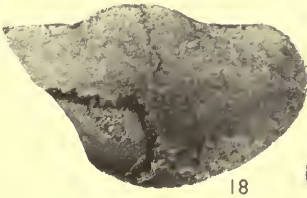
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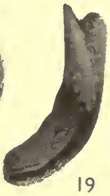
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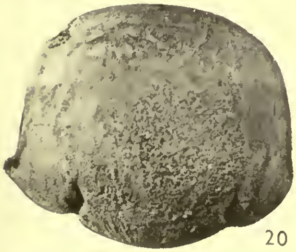
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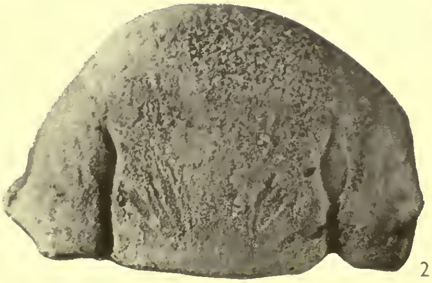
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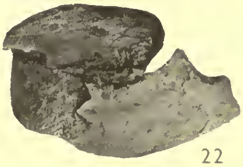
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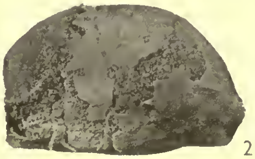
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PLATE 13

***Selenoharpes*(?) sp.**

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIGS. 1, 5, 6. Cranidium, dorsal, lateral and anterior views. In.58303. ×1·6.
FIG. 2. Cranidium, detail of fixigena and brim. In.58303. ×2·5.

***Bergamia*(?) sp.**

Shales, *D. bifidus* zone, quarry 100 yds. north of Gwredog-uchaf, Rhodogeidio.

FIG. 3. External mould of complete dorsal carapace. In.58305b. ×8·0.
FIG. 4. Internal mould of dorsal carapace lacking the librigenae. In.58306. ×1·3.
FIGS. 9, 13. External and internal moulds of cranidium and pygidium. In.58304. ×4·4.

***Ampyx* sp. (1)**

Carmel Formation, sandstones on scarp west of Bryn Gollen Uchaf, Llanerchymedd.

FIG. 8. Internal mould of cranidium. Af.824. ×3·8.

***Ampyx* sp. (2)**

Tandinas Shales, by the track 50 yds. west of Tandinas Quarry, Careg-onen.

FIG. 7. External mould of cranidium. In.58308. ×3·2.
FIG. 10. Internal mould of thoracic segments and pygidium. Af.3653. ×2·0.

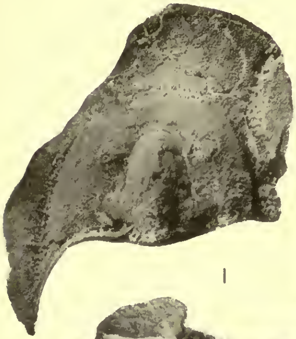
Tandinas Shales, on the shore by the power house, 100 yds. west of the pier.

FIG. 11. Internal mould of cranidium. In.58307a. ×1·7.
FIG. 12. Latex cast of external mould of pygidium. In.58309. ×3·0.

***Ceraurinella* sp.**

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIG. 14. Incomplete cranidium. In.58312. ×2·2.
FIG. 15. Glabella. In.58311. ×3·2.
FIG. 16. Glabella. In.58310. ×3·2.
FIG. 17. Hypostome. In.58315. ×2·4.
FIG. 18. Latex cast of external mould of thoracic segment. In.58316. ×2·1.
FIG. 19. Thoracic segment. In.58317. ×2·2.
FIG. 20. Pygidium. In.58318. ×4·0.
FIG. 21. Hypostome. In.58313. ×1·6.
FIG. 22. Hypostome. In.58314. ×3·2.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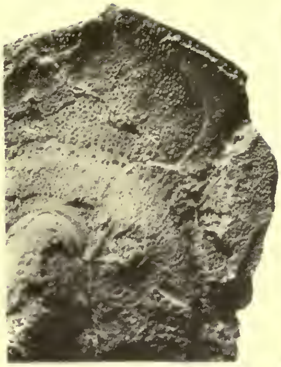
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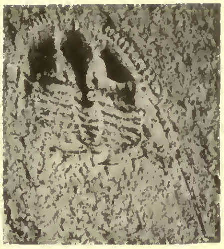
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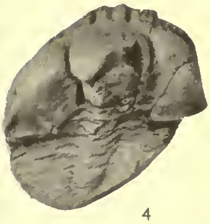
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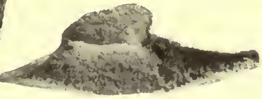
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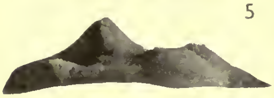
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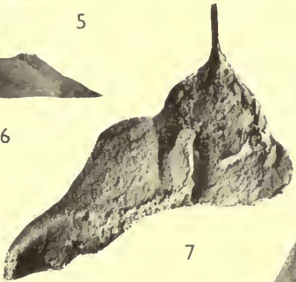
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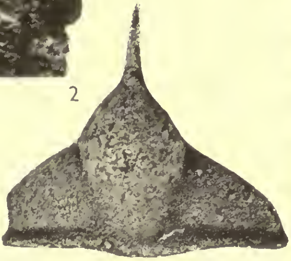
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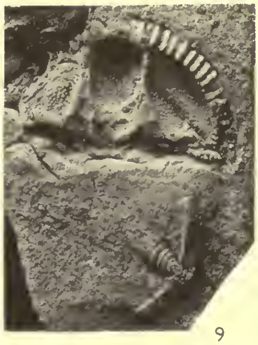
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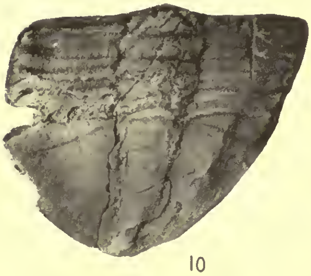
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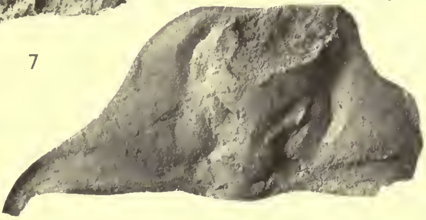
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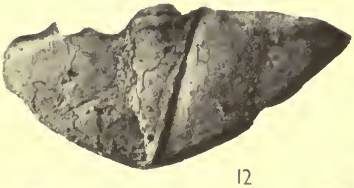
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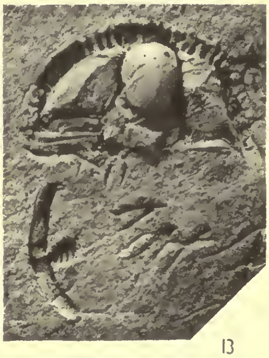
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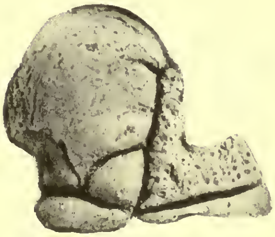
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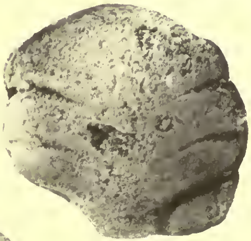
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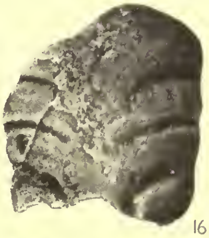
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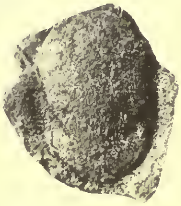
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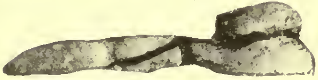
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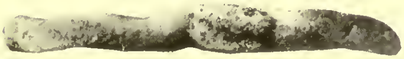
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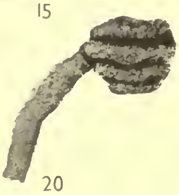
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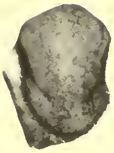
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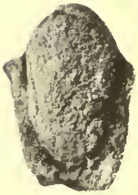
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PLATE 14

Sphaerexochus sp.

Tandinas Shales, on the shore by the power house, 100 yds. west of the pier, Careg-onen.

FIGS. 1, 2. Cranidium, dorsal and oblique lateral views. In.58319. ×3·2.

Pliomerops sp.

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIG. 3. Hypostome. In.58321. ×1·8.
FIG. 4. Incomplete cranidium. In.58320. ×2·2.
FIG. 6. Incomplete pygidium. In.58322. ×1·3.
FIG. 7. Latex cast of external mould of pygidium. In.58323b. ×2·0.

Placoparia sp.

Shales on the shore at Porth-y-gwichiaid, 80 yds. north of the streamlet.

FIG. 5. Complete dorsal carapace, lacking the librigenae. Af.1319. ×2·6.

Calymenid (s.l.) sp.

Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIG. 8. Hypostome. In.58324. ×3·1.
FIGS. 9, 12, 13. Pygidium, dorsal, posterior and oblique lateral views. In.58325. ×2·8.

Neseuretus monensis (Shirley)

Carmel Formation, sandstones 120 yds. north-west of Chwaen-bach, Llanerchymedd.

FIG. 11. Internal mould of pygidium. In.58327. ×1·7.
Carmel Formation, sandstones 440 yds. north of Ty-hen, Treiorwerth.
FIG. 16. Internal mould of pygidium. In.58326a. ×1·7.

Amphilichas sp. (1)

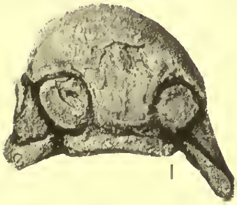
Garn Formation, limestone blocks in breccia beds, Porth Padrig, Mynachdy.

FIGS. 10, 14, 17. Cranidium, anterior, lateral and dorsal views. In.58328. ×2·0.
FIG. 15. Hypostome. In.58329. ×3·3.

Amphilichas sp. (2)

Tandinas Shales, by the track 50 yds. west of Tandinas Quarry, Careg-onen.

FIGS. 18, 19. External mould and latex cast of cranidium. Af.3000. ×2·1.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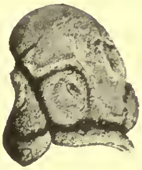
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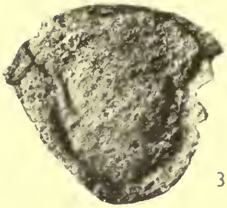
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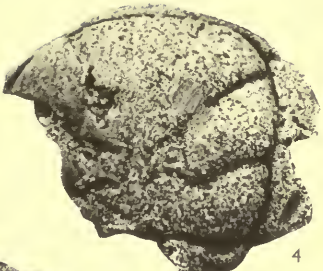
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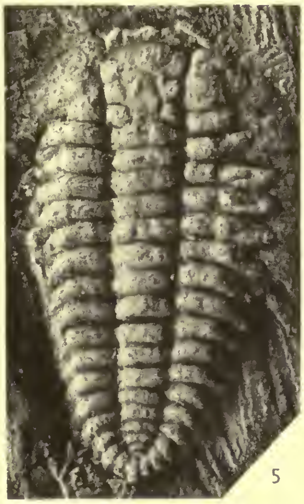
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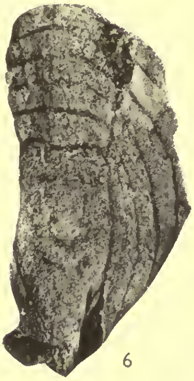
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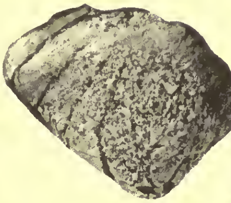
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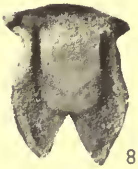
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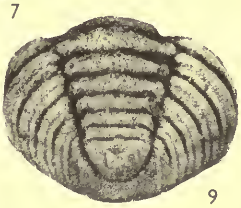
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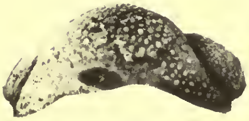
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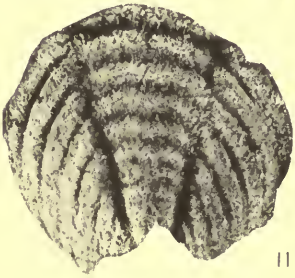
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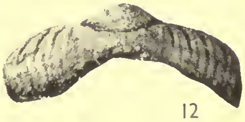
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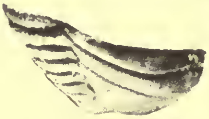
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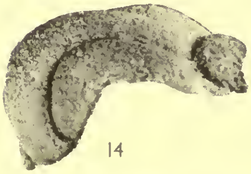
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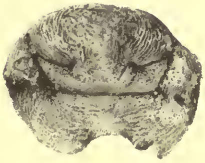
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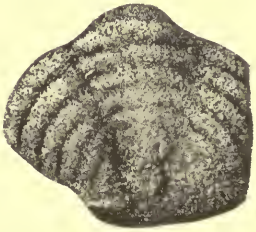
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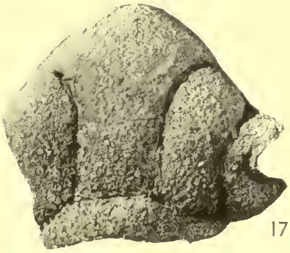
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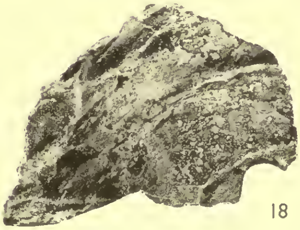
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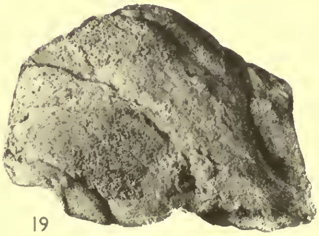
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THE CAUDAL SKELETON IN LOWER LIASSIC PHOLIDOPHORID FISHES

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NATURAL HISTORY

C. PATTERSON

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THE CAUDAL SKELETON IN LOWER LIASSIC PHOLIDOPHORID FISHES

By COLIN PATTERSON

MS accepted May 17th 1967

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SYNOPSIS

The caudal vertebrae and the caudal skeleton and fin are described in *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis*. The centra were formed by calcifications in the sheath of the unconstricted notochord, and were diplospondylous in the middle part of the caudal region. The caudal skeleton is strongly asymmetrical, resembling those of primitive actinopterygians rather than teleosts. The uroneurals of teleosts are modified ural neural arches: the ural neural arches are already considerably modified in pholidophorids. One or two urodermals, relics of the rhombic scales of the caudal axis, persist in a few primitive teleosts. The functional significance of changes in the tail at the pholidophorid/leptolepid transition is discussed, and a new definition of the Teleostei, based on these changes, is proposed.

I. INTRODUCTION

During the last few years the caudal skeleton of teleost fishes has been shown to be of great value in tracing relationships between and within major groups. This interest in the caudal skeleton is due primarily to the work of Gosline (1960) who first introduced a rational terminology for the various structures. Nybelin (1963), in a superbly illustrated paper containing the first detailed illustrations of caudal structures in fossil teleosts, gave added precision to the terminology of the tail, and paid particular attention to the nature of the " uroneurals ". Nybelin figured the caudal skeleton in several Jurassic teleost forerunners including *Leptolepis coryphaenoides*, *L. normandica* and *L. dubia*, but the structure of the tail in the ancestors of the leptolepids, the pholidophorids, has so far remained unknown. During a visit to the Royal Scottish Museum, Edinburgh, in October 1966, I came across a specimen from the Lower Lias of Lyme Regis, Dorset, identifiable as *Pholidophorus bechei*, in which the scales are missing, exposing a well preserved caudal endoskeleton. In trying to interpret this specimen I have examined the British Museum (Natural History) collections of Lower Lias pholidophorids, which have recently been revised by Nybelin (1966), and found that the caudal skeleton is occasionally visible or can be prepared in specimens of *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis*. The primary purpose of the descriptions of caudal structures in these fishes which follow is to settle the " uroneural/urodermal " question, but other points in the structure of the caudal skeleton and fin in these pholidophorids throw light on the evolution of teleosts and a discussion of these is added.

My best thanks are due to Prof. Orvar Nybelin, who has been most generous with advice, with unpublished photographs of pholidophorid caudal skeletons and unpublished information on teleost caudal skeletons, and has read the manuscript of this paper. Dr. P. H. Greenwood has also kindly read the paper in manuscript. I am grateful to Drs. C. D. Waterson and R. S. Miles of the Royal Scottish Museum for the loan of a specimen of *Pholidophorus bechei*, and to Mr. P. J. Green, who took the photographs.

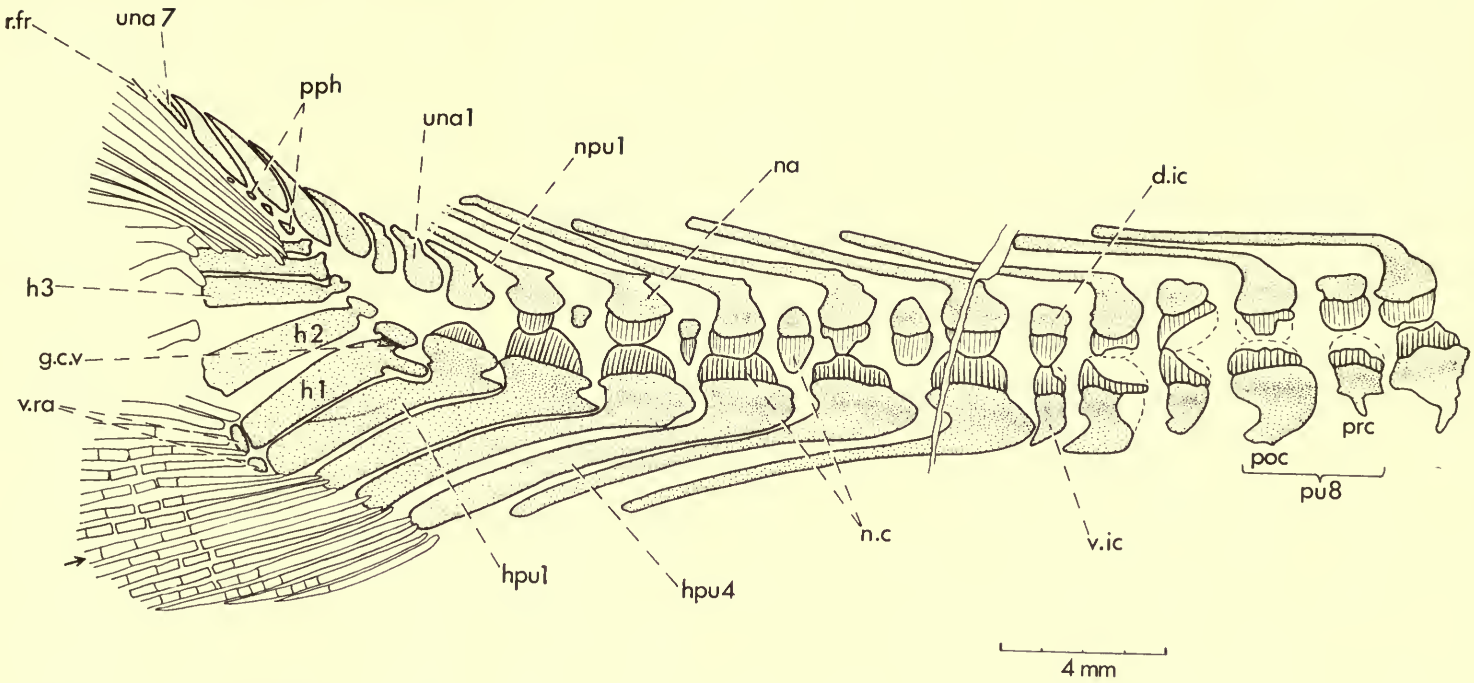
The abbreviation RSM refers to the Royal Scottish Museum, Edinburgh. Specimens referred to by a number without prefix or with the prefix " P " are in the Department of Palaeontology, British Museum (Natural History); the prefix BMNH indicates dried skeletons in the Department of Zoology, British Museum (Natural History).

II. DESCRIPTION

In this section the caudal skeleton is described in three pholidophorids from the Lower Lias of Lyme Regis, Dorset, *Pholidophorus bechei* Agassiz, *Pholidolepis dorsetensis* Nybelin, and *Pholidophoropsis maculata* Nybelin.

Pholidophorus bechei is the type species of the genus. The caudal skeleton is visible in 19010 (Pl. 1, Text-fig. 1: the skull of this specimen was figured by Rayner 1948, fig. 26), RSM 1888.61.73 (Pl. 3, fig. 1; Text-figs 2A, 5A), P.34822 (Text-figs 2B, 5B) and P.48820 (Text-fig. 5C). P.154 (Pl. 5, fig. 1) and several other specimens have also been used in preparing the description.

Pholidolepis dorsetensis Nybelin (1966 : 387) is the only species of a genus set up by Nybelin for Lower Liassic pholidophorids differing from *Pholidophorus* principally in reduction in the enamel covering of the dermal bones, loss of fulcra from all fins except the caudal, and in the presence of thin, cycloid scales. Nybelin suggested that *Pholidolepis* might be intermediate between *Pholidophorus* and *Leptolepis*. The caudal skeleton is partially visible in several specimens of *P. dorsetensis*, the best being P.6067 (Pl. 2; Text-fig. 3), P.44709 (Pl. 3, fig. 2; Text-fig. 4A) and P.939*c* (Text-fig. 4B).



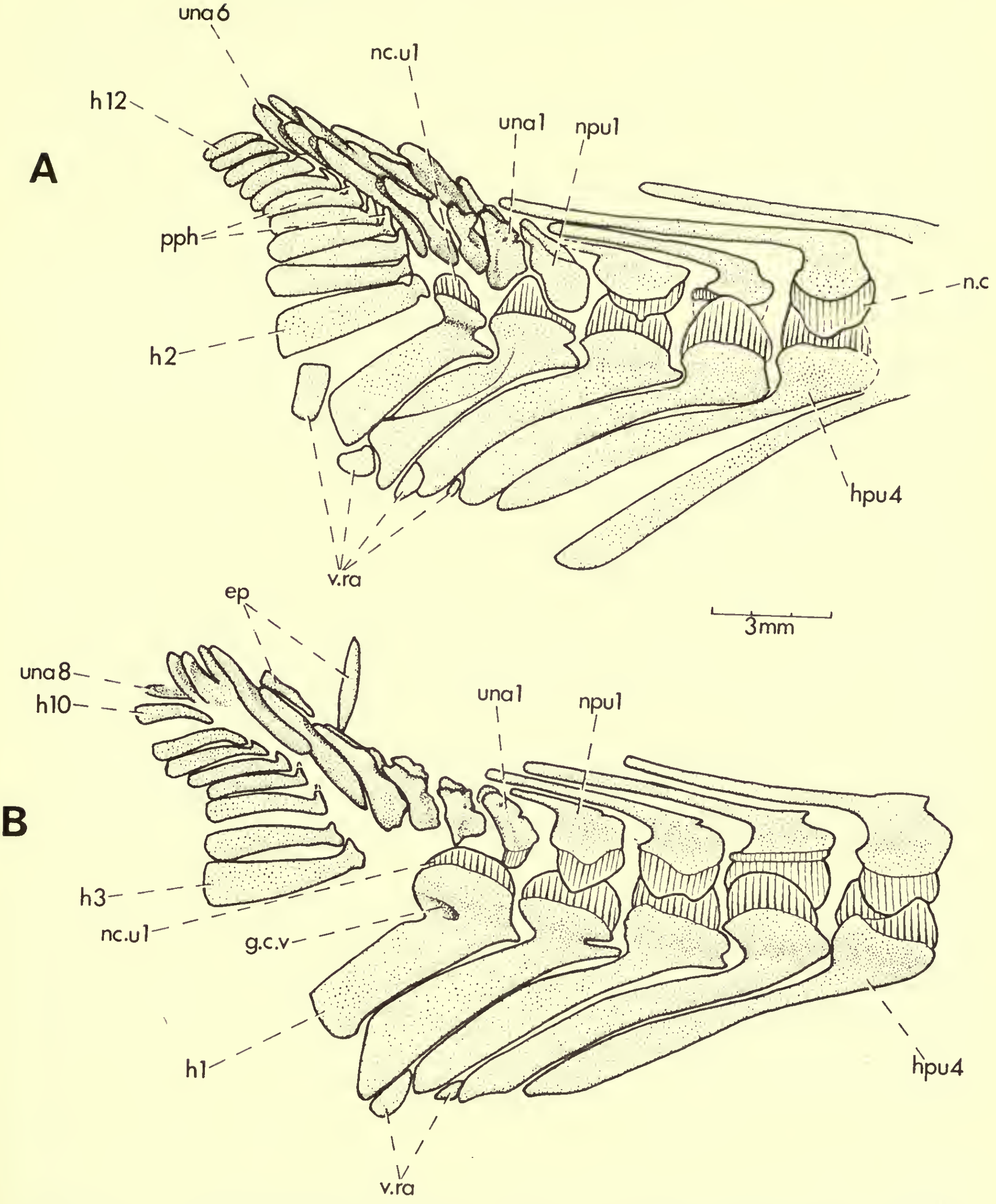
TEXT-FIG. 1. *Pholidophorus bechei* Agassiz. The posterior part of the vertebral column and the base of the caudal fin as preserved in 19010 (see also Pl. 1). *d. ic*, dorsal intercalary; *g.c.v*, groove for caudal vein and artery on first hypural; *h 1–3*, hypurals 1–3; *hpu 1*, *hpu 4*, haemal spines of first and fourth pre-ural vertebrae; *na*, neural arch; *n.c*, notochordal calcifications (hemicentra); *npu 1*, first pre-ural neural arch; *poc*, *prc*, *pu 8*, postcentrum and precentrum of eighth pre-ural vertebra; *pph*, postero-dorsal processes on heads of upper hypurals; *r.fr*, reduced uppermost hypaxial fin-ray; *una 1*, *una 7*, first and seventh ural neural arches; *v.ic*, ventral intercalary; *v.ra*; ventral caudal radials. An arrow marks the lowermost principal caudal ray.

The genus *Pholidophoropsis* Nybelin (1966 : 411) contains Lower Liassic pholidophorids in which the scales are thin and cycloid and the dermal bones with little enamel as in *Pholidolepis*, but which in other respects resemble *Pholidophoroides*. There are two species, *P. caudalis* (Woodward) and *P. maculata* Nybelin. In *P. caudalis* the caudal skeleton is not well exposed in any available specimen, but the caudal squamation is well shown in the holotype, 43055 (Text-fig. 8). The paratype of *P. maculata*, P.7582 (Pl. 4; Text-fig. 6) has the caudal skeleton somewhat disturbed but otherwise well preserved.

(a) *Distinction between ural and pre-ural structures.* Nybelin (1963 : 487) introduced the distinction between pre-ural centra, carrying normal or little modified haemal arches and spines, and ural centra, carrying hypurals. The boundary between these is marked by the point at which the caudal artery and vein, carried within the haemal arches of the pre-ural vertebrae, fork and pass lateral to the hypurals, which do not have a median canal proximally. 19010, *Pholidophorus bechei*, is the only available specimen in which the axial skeleton is preserved in the round. In this specimen (Pl. 1; Text-fig. 1) the exit of the caudal vessels from the haemal canal is marked by a horizontal groove (*g.c.v.*) on the first hypural (*h 1*). Just below this groove on the first hypural there is a peg-like process passing forwards and fitting in a notch on the hind face of the first pre-ural haemal arch (*hpu 1*). The succeeding hypurals are without such a process while the two last haemal arches have a less distinct process. A similar peg-like process can be recognized on the first hypural of *Leptolepis coryphaenoides* and *L. normandica* (Nybelin 1963, text-figs 9, 10), *L. dubia* (Text-fig. 10), *Salmo*, etc., and in pholidophorids it is a useful means of recognizing the first hypural in specimens where the caudal skeleton is too crushed to show the groove for the caudal vessels. In P.34822 (Text-fig. 2B) the groove for the caudal vessels on the first hypural is partially covered, forming a canal anteriorly.

The validity of the ural/pre-ural dividing line as a morphological boundary is supported by the fact that in pholidophorids the pre-ural neural arches are fused with the neural spines into median structures while the ural neural arches are paired (p. 210).

(b) *The vertebral centra.* The vertebral column is best preserved in 19010, *Pholidophorus bechei* (Pl. 1; Text-fig. 1). The notochord was unconstricted. Above and below the space occupied by the notochord there is a series of calcifications in the form of half-rings (*n.c*), normally lying opposite one another in dorso-ventral pairs which meet or almost meet lateral to the notochord. The neural and haemal arches, and in the middle part of the caudal region the independent dorsal and ventral intercalaries (*d.ic, v.ic*; terminology of Schaeffer 1967), are applied to the half-ring calcifications dorso-laterally and ventro-laterally, but do not cover them laterally. As preserved, these calcifications (hemicentra) differ sharply from the endochondral bone of the neural and haemal arches in their dark colour, dense, fibrous texture and vertical striation (Pl. 1). In thin section the hemicentra differ from the trabecular, sparsely cellular bone of the arches in being solid, without cell spaces or vascular canals, and in containing many tangentially arranged fibres, which presumably account for their dark colour and vertically striated appearance.

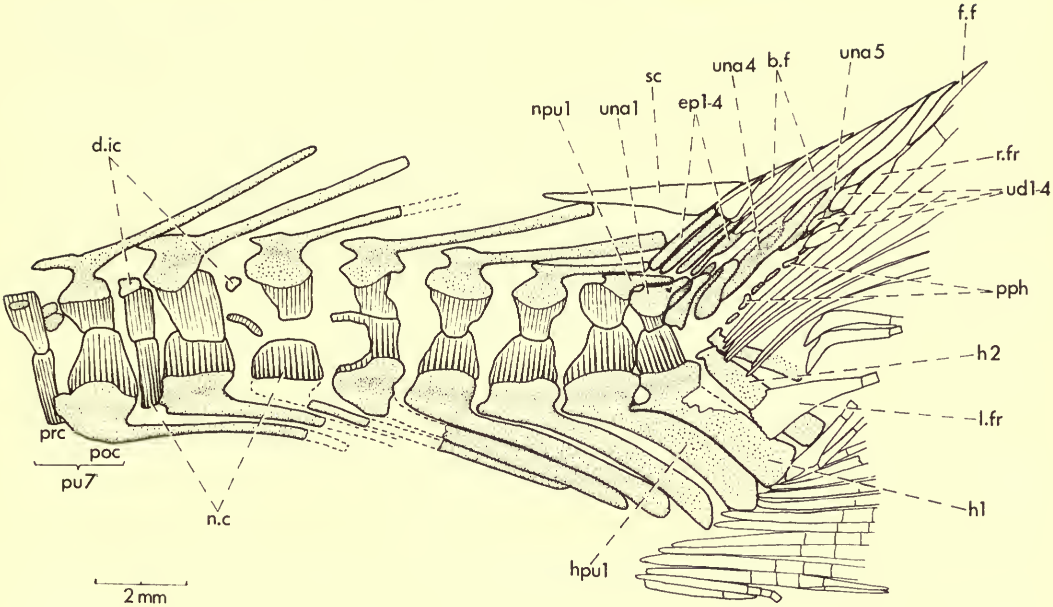

A
una 6
nc.u1
h12
una1
npu1
pph
n.c
h2
hpu4
v.ra
3mm
B
ep
una8
h10
una1
npu1
h3
nc.u1
g.c.v
h1
hpu4
v.ra

TEXT-FIG. 2. *Pholidophorus bechei* Agassiz. The caudal skeleton as preserved in A, RSM 1888.61.73 (see also Pl. 3, fig. 1); *B*, P.34822. Details of the ural neural arches of these specimens are shown in Text-fig. 5. In *B* the second hypural is missing. *ep*, epurals; *g.c.v*, groove for caudal vessels on first hypural; *h 1*, *h 2*, *h 3*, *h 10*, *h 12*, hypurals 1–12; *hpu 1*, *hpu 4*, first and fourth pre-ural haemal spines; *n.c*, notochordal calcifications (hemicentra); *nc.u 1*, ventral hemicentrum of first ural centrum; *npu 1*, first pre-ural neural arch; *pph*, postero-dorsal processes on heads of upper hypurals; *una 1*, *una 6*, *una 8*, first, sixth and eighth ural neural arches; *v.ra*, ventral caudal radials

In structure these hemicentra agree exactly with the centra of the Triassic pholidopleurid *Australosomus* (Stensiö 1932 : 174, pls 35–37). Stensiö concluded that the ring-like centra of *Australosomus* are chordal, not perichordal as are the centra of most actinopterygians. Nielsen (1949 : 134, pl. 6) found that in one specimen of *Australosomus* the small precentra in the diplospondylous middle part of the caudal region consisted of independent dorsal and ventral half-rings, just as in *P. bechei*. The structure and arrangement of the centra in *P. bechei* shows that, like the centra of *Australosomus*, they are calcifications in the sheath of the notochord: this interpretation is supported by the presence of ring-like calcifications in the sheath of the notochord of larval *Clupea* (Ramanujam 1929 : 377) and by the recent discovery (François 1966 : 292) that in *Salmo* the first calcification of the centrum (in ontogeny) is a median ventral crescentic calcification in the sheath of the notochord. In *Pholidophorus bechei* and in *Pholidophoropsis* the dorsal and ventral hemicentra appear to be separate throughout the vertebral column, but in *Pholidolepis* they tend to fuse with each other to form complete rings (Text-fig. 4A).

In *Pholidophorus bechei*, *Pholidophoropsis* and *Pholidolepis* the vertebral column is diplospondylous in the middle part of the caudal region, as it is in *Australosomus* and many holosteans. In *P. bechei* (Pl. 1; Text-fig. 1) about twelve vertebrae are diplospondylous, the majority of the caudal vertebrae. Passing forwards from the tail, the last complete precentrum (*prc*) (carrying no neural or haemal spine, Schaeffer 1967) lies in front of the sixth pre-ural centrum and in front of this there are about seven more segments in which separate pre- and postcentra (*poc*) are developed. In front of the second to fifth pre-ural centra there are no independent ventral intercalaries or ventral notochordal calcifications, but the dorsal intercalaries remain free, all but the last with a small notochordal calcification. In *Pholidolepis* (Pl. 2; Text-fig. 3), although the vertebral column is never so well preserved as it is in some specimens of *P. bechei*, the number of diplospondylous segments seem to be about the same as in *P. bechei*: 38163 shows complete precentra in front of pre-ural centra 7–15, though other specimens show fewer precentra. In *Pholidophoropsis* there are at least five diplospondylous segments (pre-ural 6–10) in P.7582, *P. maculata*. In these pholidophorids it is impossible to be certain whether the intercalaries fused with the neural and haemal arches or were absent in centra which are not diplospondylous. Appearances in *P. bechei* (Text-fig. 1) and *Pholidolepis* (Text-fig. 3) suggest that the ventral intercalaries fuse with the haemal arch of the centrum behind them, but it is quite possible that intercalaries were absent in monospondylous segments, as they appear to be in teleosts.

In *P. bechei* the last complete centrum, with both dorsal and ventral notochordal calcifications, is the second pre-ural in 19010 (Text-fig. 1), the first pre-ural in RSM 1888.61.73 (Text-fig. 2A) and the first ural in P.34822 (Text-fig. 2B) and other specimens. In 19010 there is only a ventral hemicentrum in the first pre-ural centrum, and in RSM 1888.61.73 there is only a ventral hemicentrum in the first ural centrum, above the first hypural. In all specimens the notochord was uncalcified and unconstricted behind the first hypural, though the close approximation of the heads of the hypurals and the neural arches in the posterior ural region (Text-figs 1, 2) shows that the notochord must have decreased in diameter very sharply.



TEXT-FIG. 3. *Pholidolepis dorsetensis* Nybelin. The posterior part of the vertebral column and the base of the caudal fin as preserved in P.6067 (see also Pl. 2). *b.f.* epaxial basal fulcra; *d.ic*, dorsal intercalaries; *ep 1–4*, epurals; *f.f.*, fringing fulcra; *h 1*, *h 2*, first and second hypurals; *hpu 1*, haemal spine of first pre-ural centrum; *l.fr*, expanded base of lowermost fin-ray in upper caudal lobe; *n.c*, notochordal calcifications (hemicentra); *npu 1*, neural arch of first pre-ural centrum; *poc*, *prc*, *pu 7*, postcentrum and precentrum of seventh pre-ural vertebra; *pph*, postero-dorsal processes on heads of upper hypurals; *r.fr*, reduced uppermost hypaxial fin-ray; *sc*, upper caudal scute; *ud 1–4*, urodermals; *una 1*, *una 4*, *una 5*, first, fourth and fifth ural neural arches.

In *Pholidolepis* the last complete centrum is the first pre-ural in some specimens, but is normally the first ural (Text-figs 3, 4): behind this point the notochord was uncalcified and must have decreased in diameter more sharply than in *P. bechei*, for the gap between the hypurals and the ural neural arches seems normally to be obliterated at the level of the fourth hypural. In *Pholidophoropsis* both *P. caudalis* and *P. maculata* (Text-fig. 6) show a series of small notochordal calcifications extending back into the ural region, in the paratype of *P. maculata* (Text-fig. 6) to the level of the eighth hypural (*nc. u 8*).

(c) *The hypurals and haemal spines.* In *P. bechei* (Pl. 3, fig. 1, Text-figs 1, 2) the last four haemal spines (*hpu 1–4*) are broad, long and in contact wtih their neighbours, and support the foremost caudal fin-rays. The last three haemal spines and the first hypural each bear a small triangular or rhomboid distal element (*v.ra*), increasing in size from front to rear. Three to five similar distal bones or cartilages (presumably homologous with those of *Pholidophorus*) are present in *Acipenser* (Whitehouse 1910, pl. 47, fig. 2; Schmalhausen 1912, pl. 15, fig. 12), *Polyodon*

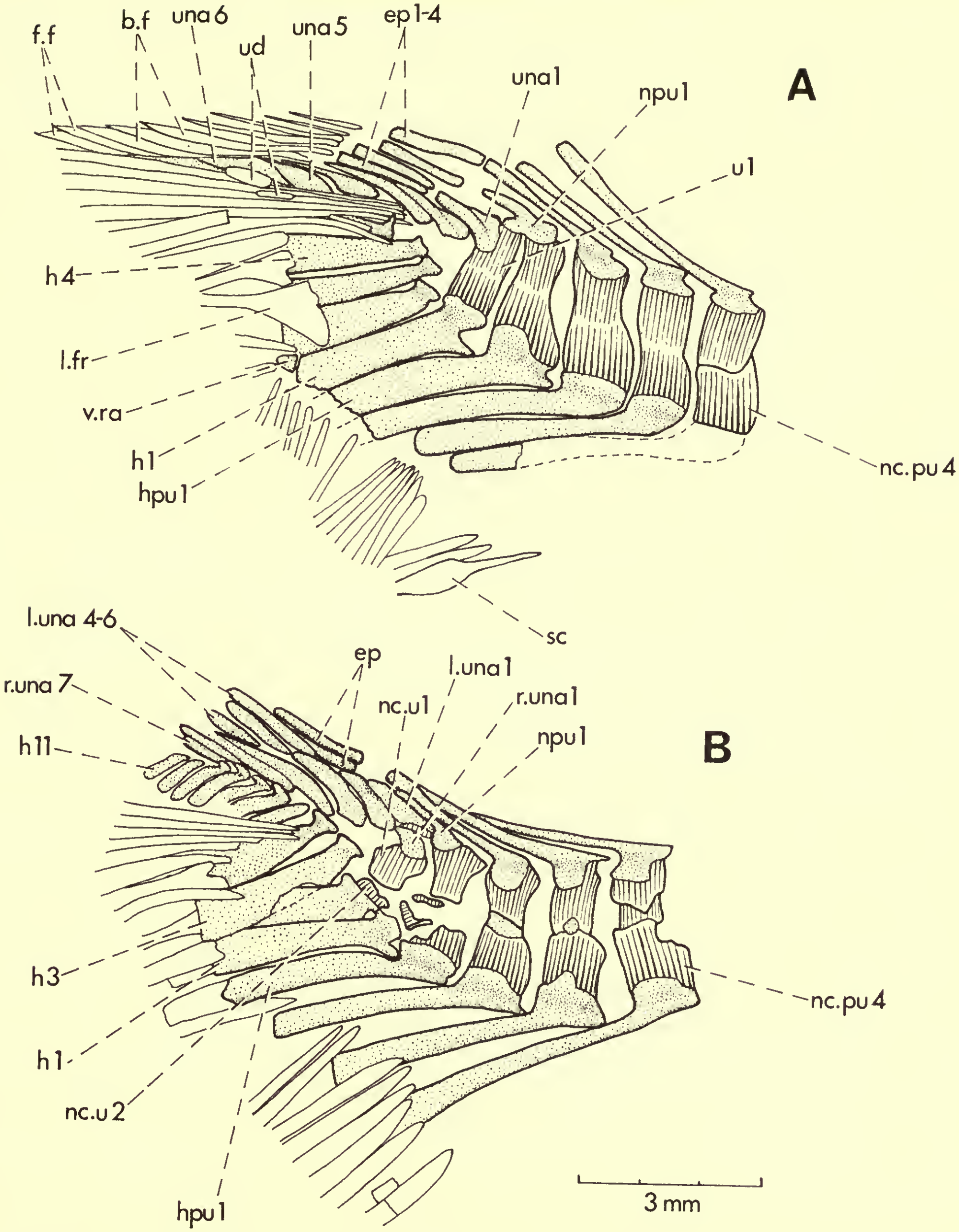
(Whitehouse 1910, pl. 47, fig. 3), *Pteronisculus* (Nielsen 1942, fig. 50) and *Boreosomus* (Nielsen 1942 : 357): they represent the radials of the hypochordal lobe of the fin. There has been considerable argument in the past on the question of the composition of the hypurals in teleosts; whether they contain radial elements or not. In *Pholidophorus*, *Polyodon*, *Pteronisculus* and *Acipenser* the ventral caudal radials are very similar in size, shape and number, and in the ontogeny of *Acipenser* they resemble those of the adult when they first appear (Schmalhausen 1912). Separate or partially separate elements in some teleost embryos have been interpreted as ventral caudal radials (Schmalhausen 1912, Totton 1914), but these do not resemble the ventral radials in *Acipenser* and *Pholidophorus* and are not always present even in primitive teleost embryos. It seems probable that teleosts (see footnote, p. 219) and living holosteans have lost the ventral caudal radials and that the hypurals are not compound structures.

Both in *Pholidolepis* and *Pholidophoropsis* the last four haemal spines are enlarged and support caudal fin-rays, as in *P. bechei*, and at least in *Pholidolepis* (35725, 35562, *v.ra*, Text-fig. 4A) separate hypochordal radial elements were present like those of *P. bechei*.

In *P. bechei*, *Pholidolepis* and *Pholidophoropsis*, as in teleosts, the lower lobe of the forked caudal fin is supported by two hypurals (*h1*, *h2*), the second more slender than the first. In *P. bechei* there are ten upper hypurals (Text-fig. 2A, *h 3–12*), decreasing gradually in length and breadth. In *Pholidolepis* there appear to be only nine upper hypurals (Text-fig. 4B, *h 3–11*). In *Pholidophoropsis* the hypurals are visible only in P.7582, *P. maculata* (Text-fig. 6), where there are nine upper hypurals (*h 3–11*), one less than in *P. bechei*.

In all three genera, but especially in *P. bechei*, the heads of hypurals 4–8 have raised postero-dorsal processes (*p.p.h*) of dense, glossy bone, very like that of the scales and dermal bones in appearance (Pl. 5, fig. 1).

(d) *The neural arches and neural spines.* In *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis* (Text-figs 1–4, 6) the neural spines of the last three pre-ural centra decrease in length progressively so that they all end at approximately the same level, the neural spine of the first pre-ural centrum (*npu 1*) being very short. The neural arches and spines of these last pre-ural centra (best seen in Text-fig. 6, *Pholidophoropsis maculata*, *npu 1*, *npu 2*) are median unpaired structures, in the shape of an inverted " Y ". The succeeding neural arches of the ural region (ural neural arches) are all separate, paired structures, without median neural spines (Text-fig. 5). These paired ural neural arches are rather complex, variable structures. There are up to eight pairs in *Pholidophorus bechei* (*l. una 8*, *r.una 8*, Text-fig. 5) and *Pholidophoropsis* (*una 8*, Text-fig. 6), but the number of ural neural arches is clearly variable since in P.48820 (*P. bechei*, Text-fig. 5C), where the series is complete and well preserved, there are seven on the right side and eight on the left. *Pholidolepis* is not known to have more than seven pairs of ural neural arches (*r.una 7*, Text-fig. 4B). The detailed structure of the ural neural arches is best seen in *Pholidophorus bechei* (Text-fig. 5) but the following description also applies to *Pholidophoropsis* and *Pholidolepis*. The first ural neural arch (*l. una 1*, *r.una 1*,

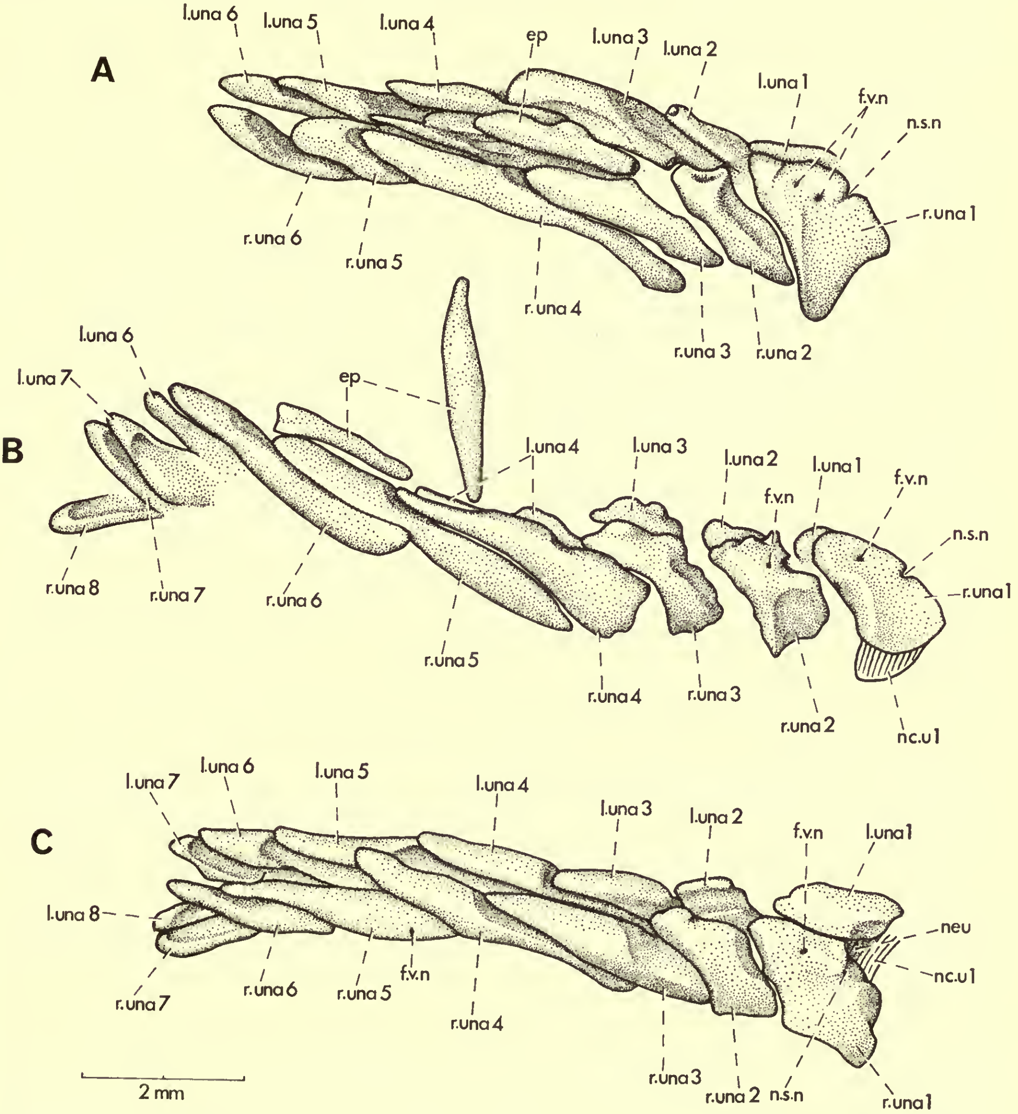

f.f
b.f
una 6
ud
una 5
ep 1-4
una 1
npu 1
A
u 1
h 4
l.fr
v.ra
h 1
hpu 1
nc.pu 4
sc
l.una 4-6
r.una 7
h 11
ep
l.una 1
nc.u 1
r.una 1
npu 1
B
h 3
h 1
nc.u 2
hpu 1
nc.pu 4
3 mm

Text-fig. 4. *Pholidolepis dorsetensis* Nybelin. The caudal skeleton as preserved in *A*, P.44709 (see also Pl. 3, fig. 2); *B*, P.939c. *b.f*, basal fulcra; *ep 1–4*, epurals, *f.f*, fringing fulcra; *h 1*, *h 3*, *h 4*, *h 11*, hypurals 1–11; *hpu 1*, haemal spine of first pre-ural centrum; *l.fr*, expanded base of lowermost fin-ray of upper caudal lobe; *l.una 1–6*, ural neural arches of left side; *nc.pu 4*, notochordal calcification (hemicentrum) of fourth pre-ural vertebra; *nc.u 1*, *nc.u 2*, notochordal calcifications (hemicentra) of first and second ural centra; *npu 1*, neural arch of first pre-ural vertebra; *sc*, ventral caudal scute; *r.una 1–7*, ural neural arches of right side; *u 1*, first ural centrum; *ud*, urodermals; *una 1–6*, ural neural arches; *v.ra*, ventral caudal radial.

Text-fig. 5; *una 1*, Text-figs 1, 3, 4, 6) corresponds fairly closely with the first pre-ural neural arch (*npu 1*) in shape and size, but is deeper. A notch (*n.s.n*) is usually visible on the anterior margin of the first ural neural arch. This notch corresponds with a notch on the anterior edge of the pre-ural neural arches and must mark the passage of the segmental spinal nerve, or at least of the dorsal root of the nerve. Approximately in the centre of the lateral face of the first ural neural arch, a little above the level of the notch for the spinal nerve, there is usually a small foramen (*f.v.n*, Text-fig. 5B, C, also seen in *Pholidolepis*, Text-fig. 3) which is occasionally double (Text-fig. 5A). Since similar foramina are sometimes present in more posterior ural neural arches (the second in Text-fig. 5B, the fifth in Text-fig. 5C) these foramina are probably vascular and without general significance. The second ural neural arch (*l.una 2*, *r.una 2*, Text-fig. 5) is variable in shape, though always shorter (rostro-caudally) than the first, and is always hollowed antero-laterally to receive the postero-medial surface of the first ural neural arch. Sometimes (Text-fig. 5B, *P. bechei*; Text-fig. 6, *Pholidophoropsis*) the second ural neural arch has an anterior notch for the spinal nerve. In *Pholidolepis* the second ural neural arch is usually produced into a slender postero-dorsal process, curving back above the third arch (Text-fig. 4A). The ural neural arches behind the second are even more variable in shape and are difficult to homologize from one specimen to another. The most important feature of these more posterior ural neural arches is that they are elongated into slender splints, each arch extending back above its successor and forwards below its predecessor. An anterior notch for the spinal nerve is occasionally present on the third ural neural arch (Text-figs 5B, 6) but is never found on more posterior arches. The posterior ural neural arches consist of two regions: the anterior region is hollowed antero-dorsally, receiving the posterior region of the preceding arch in this hollow, while the posterior region is rod-like and fits in the hollow of the succeeding arch. The anterior region of the arch is best developed in the arches in the middle part of the series and extends antero-ventrally around the space occupied in life by the narrow posterior part of the notochord. The rod-like posterior region of the arch is also best developed in the middle part of the series, becoming very short in the last one or two ural neural arches. In *Pholidophorus bechei* the longest of the seven or eight ural neural arches is the fourth (Text-fig. 5A) or the fifth (Text-fig. 5B). In *Pholidolepis* (Text-figs 3, 4) the fourth of the seven ural neural arches is the longest. In *Pholidophoropsis maculata* (Text-fig. 6) the fifth to seventh ural neural arches are equally long. In *P. bechei*, *Pholidolepis* and *Pholidophoropsis*, although the posterior ural neural arches consist internally of cancellous endochondral bone, their exposed lateral surfaces are composed of dense, glossy bone resembling in texture the postero-dorsal processes on the heads of some of the upper hypurals and the scales and fin-rays (Pl. 5, fig. 1).

(e) *The epurals*. In teleosts " epural " is the name given to a series of median bones lying behind the last complete neural spine, and supporting epaxial fin-rays. In teleosts the epurals do not seem to exceed three in number except in occasional abnormal individuals. The homologies of the epurals are discussed on p. 220.

In *Pholidophorus bechei* no specimen shows a complete series of epurals well, but in P.154 (Pl. 5, fig. 1) there are three epurals (*ep 1–3*), of which the third is the thickest, above the anterior ural neural arches, and traces of a shorter slender fourth epural (*ep 4*) behind these. The stout third epural and short slender fourth epural of this specimen probably correspond with the two epurals preserved in P.34822


A
l.una 6
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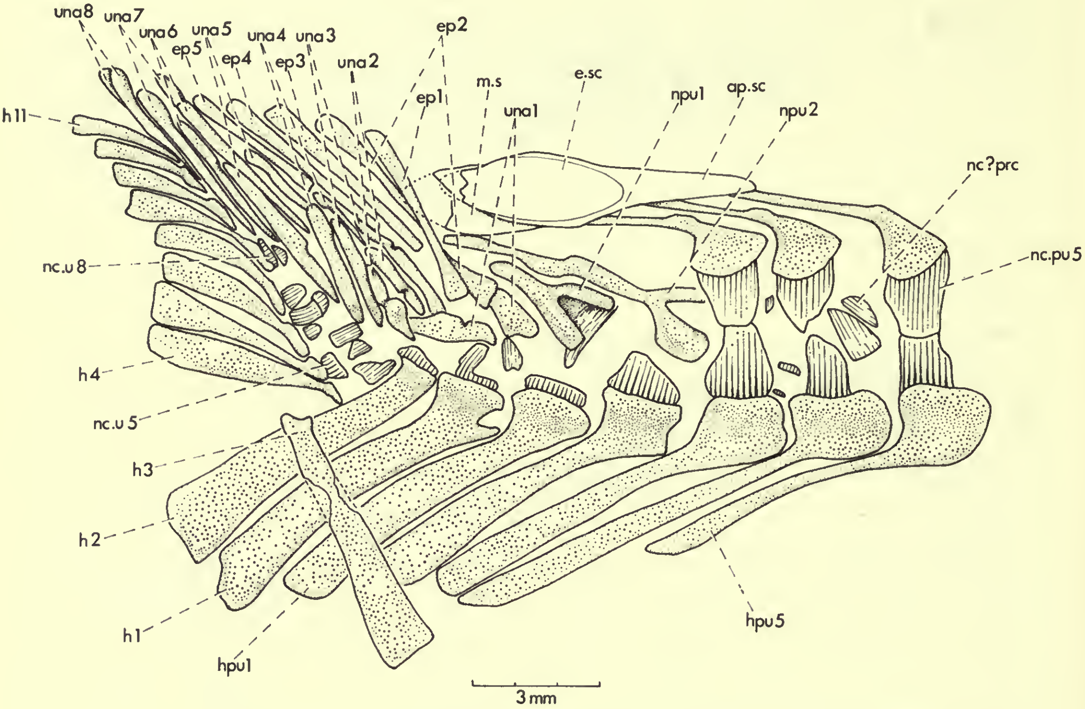
l.una 3
l.una 2
l.una 1
f.v.n
n.s.n
r.una 1
r.una 6
r.una 5
r.una 4
r.una 3
r.una 2
B
l.una 6
l.una 7
ep
l.una 4
l.una 3
l.una 2
l.una 1
f.v.n
f.v.n
n.s.n
r.una 1
r.una 8
r.una 7
r.una 6
r.una 5
r.una 4
r.una 3
r.una 2
nc.u 1
C
l.una 7
l.una 6
l.una 5
l.una 4
l.una 3
l.una 2
f.v.n
l.una 1
l.una 8
neu
nc.u 1
r.una 7
r.una 6
r.una 5
f.v.n
r.una 4
r.una 3
r.una 2
n.s.n
r.una 1
2 mm

Text-fig. 5. *Pholidophorus bechei* Agassiz. The ural neural arches as preserved in *A*, RSM 1888.61.73; *B*, P.34822; *C*, P.48820. *ep*, epurals; *f.v.n*, foramina, probably vascular, in the ural neural arches; *l.una 1–8*, first—eighth ural neural arches of left side; *nc.u 1*, dorsal notochordal calcification of first ural centrum; *neu*, neural canal; *n.s.n*, notch for spinal nerve on first ural neural arch; *r.una 1–8*, first—eighth ural neural arches of right side.

(*ep*, Text-fig. 5B). In *Pholidolepis* there are four epurals (*ep 1–4*, Text-figs 3, 4A) lying above the first ural and first pre-ural neural arches. In *Pholidophoropsis maculata*, P.7582 shows five long epurals (*ep 1–5*, Text-fig. 6), the first four originating at the tips of the first ural and first pre-ural neural arches, the fifth at the tip of the fourth ural neural arch.



Text-fig. 6. *Pholidophoropsis maculata* Nybelin. The caudal skeleton as preserved in P.7582 (see also Pl. 4). *ap.sc*, anterior process of upper caudal scute; *ep 1–5*, epurals; *e.sc*, enamelled area of upper caudal scute; *h 1*, *h 2*, *h 3*, *h 4*, *h 11*, hypurals 1–11; *hpu 1*, *hpu 5*, haemal spines of first and fifth pre-ural vertebrae; *m.s*, dorsal median scale; *nc ? prc*, notochordal calcification, probably of poorly preserved precentrum; *nc.pu 5*, notochordal calcification (hemicentrum) of fifth pre-ural centrum; *nc.u 5*, *nc.u 8*, notochordal calcifications of fifth and eighth ural centra; *npu 1*, *npu 2*, neural arches of first and second pre-ural vertebrae; *una 1–8*, first to eighth ural neural arches.

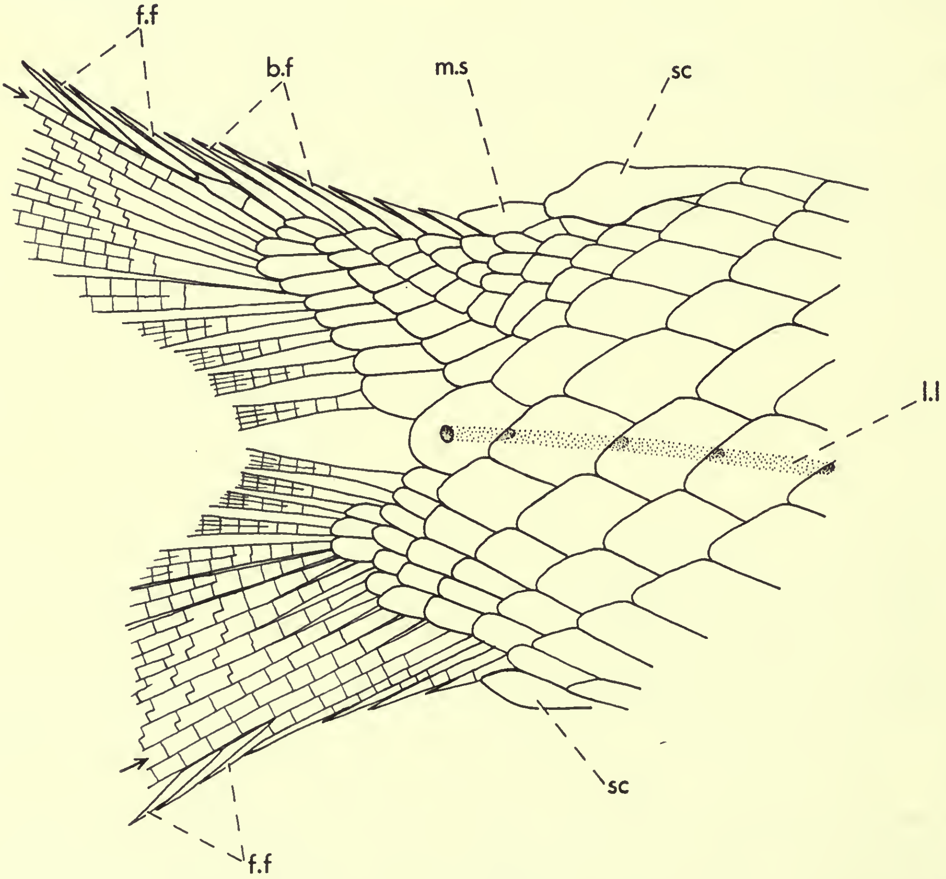
(f) *The fin-rays.* In *Pholidophorus bechei* the caudal fin contains twenty-two to twenty-four principal fin-rays (Text-fig. 7), with the outermost ray in each lobe unbranched and ten or (normally) eleven branched rays in each lobe. Preceding the lowermost principal rays there are six or seven unbranched but segmented rays, grading into fringing fulcra (*f.f*) posteriorly. The uppermost hypaxial fin-ray is much reduced (*r.fr*, Text-figs 1, 7) ending at a notch on the edge of the uppermost principal ray at the level of the first fringing fulcra. This reduced uppermost ray is usually segmented once. The epaxial lobe of the fin is represented only by six or seven basal fulcra (*b.f*), paired, unsegmented structures, grading posteriorly into fringing fulcra (*f.f*) inserted on the upper face of the uppermost principal ray. The seven upper principal rays are very deeply cleft basally, the slender, unsegmented proximal ends crossing the upper hypurals almost at right angles, and ending at the level of the third or fourth hypural (Text-fig. 1; Pl. 1, Pl. 5, fig. 1). The postero-dorsal processes (*p.p.h*) on the heads of the upper hypurals lie against the base of the upper fin-ray. The fin-rays of the lower lobe of the tail are much less deeply cleft and only cover the tips of the lower hypurals and the haemal spines (Text-fig. 1). The proximal end of the innermost ray in each lobe of the fin is expanded, as in *Leptolepis coryphaenoides* and *L. normandica* (Nybelin 1963, figs 9, 10) and various teleosts. The foremost fin-rays in the lower lobe of the fin articulate with the fourth pre-ural haemal spine, and the rays of the lower lobe are equally distributed on the last four haemal spines and the first hypural; the second hypural appears to carry only a single fin-ray, as it does in most teleosts.

In *Pholidolepis* there are twenty to twenty-one principal caudal fin-rays, the outermost in each lobe unbranched, the upper lobe with nine branched rays and the lower with nine or ten: in this *Pholidolepis* is closer than *Pholidophorus* to the primitive teleostean count of nine branched rays in the upper lobe, eight in the lower. In *Pholidolepis*, as in *P. bechei*, there are about six small rays in front of the lower principal rays, the foremost articulating with the fourth pre-ural haemal spine, the seven uppermost hypaxial rays are deeply cleft basally, crossing the upper hypurals and ending on the third hypural (Pl. 2; Text-fig. 3) and the dorsal margin of the fin bears fulcra throughout its length. Nybelin (1966 : 392) was unable to find fulcra on the ventral margin of the tail in *Pholidolepis*, and some specimens, including the holotype, were clearly without them, but in 35725 (paratype), 38163 and P.6067 there are fulcra on the visible parts of the lower edge of the fin. A much reduced uppermost hypaxial fin-ray (*r.fr*, Text-fig. 3) is usually present, as in *Pholidophorus bechei*, but in *Pholidolepis* it is unsegmented. The proximal ends of the innermost fin-rays are expanded, as in *P. bechei*, but in *Pholidolepis* the base of the innermost ray of the upper lobe of the fin, articulating with the third hypural, is much larger than its neighbours (*l.fr*, Text-figs 3, 4A), as in *Leptolepis dubia* (Text-fig. 10) and *Elops* (Nybelin 1963, text-fig. 4).

In *Pholidophoropsis* the number of principal caudal rays is greater than in *Pholidophorus bechei*: in *P. caudalis* there are twenty-five, in *P. maculata* twenty-six to twenty-seven, both species having five small rays in front of the lower principal rays. The two uppermost principal rays are normally unbranched, the lowermost one is often branched. There is no reduced uppermost hypaxial ray such as is present in *P. bechei* and *Pholidolepis*: the unbranched uppermost ray obviously represents this ray in its unreduced condition. The upper hypaxial fin-rays cover the upper hypurals, as in *P. bechei* and *Pholidolepis*. Both margins of the fin carry fulcra throughout their length.

(g) *The squamation.* In *Pholidophorus bechei* the scales are thick, rhombic and enamelled, and scales of this type cover the caudal endoskeleton and the bases of the fin-rays completely (Text-fig. 7). The scaling of the upper lobe of the fin is more extensive than that of the lower, *P. bechei* retaining a vestige of the scaled body lobe of the tail in more primitive actinopterygians. Preceding the basal fulcra (*b.f*) on the upper margin of the fin, which are paired structures, there are two or three median scales (*m.s*), the anterior one (*sc*) scute-like, with a long tapering anterior process (P.3586*e*). On the lower lobe of the fin the small anterior fin-rays are preceded by at least one median scale (*sc*) (38107), probably similar in shape to the scute-like dorsal median scale.

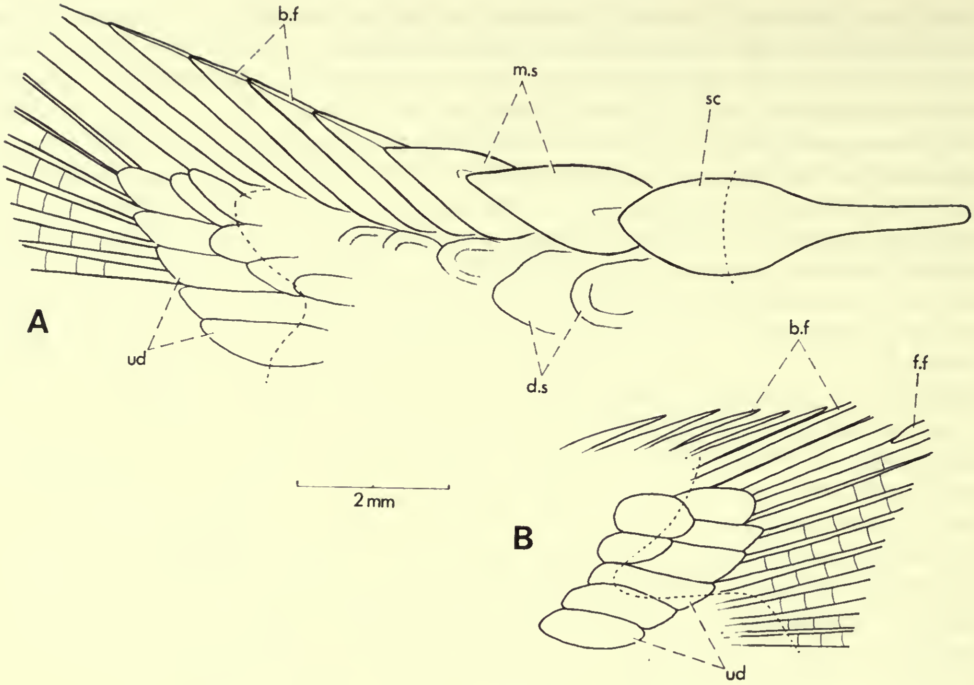
In *Pholidolepis* the trunk scales are thin, cycloid, and without enamel (Nybelin 1966 : 391). In front of the basal fulcra on the upper margin of the caudal fin (*b.f*, Text-fig. 3) there is a thick, median scale with a slender anterior process (29010,



Text-fig. 7. *Pholidophorus bechei* Agassiz. Restoration of the squamation of the caudal region and the base of the caudal fin, based on several specimens. The squamation is drawn as if folded out flat, with the dorsal and ventral median scales shown in surface view. × 3 approx. *b.f*, epaxial basal fulcra; *f.f*, fringing fulcra; *l. l*, course of lateral line; *m.s*, median dorsal scale; *r.fr*, reduced uppermost hypaxial fin-ray; *sc*, upper and lower caudal scutes. Arrows indicate the uppermost and lowermost principal fin-rays.

P.6067 : *sc*, Text-fig. 3), clearly homologous with the similar scale in *Pholidophorus bechei* and in primitive teleosts (Gosline 1965, Patterson, in press). Gosline refers to this median scute-like structure in teleosts as a fulcral scale, but since it is apparently homologous neither with the basal fulcra nor the fringing fulcra it will be referred to here as a caudal scute. Like the urodermals of teleosts (see p. 230) it represents an almost unmodified relic of the thick, rhombic scales of pholidophorids. In *Pholidolepis* the greater part of the caudal scute is covered by thin, cycloid scales, and as in teleosts, it is without enamel. A similar but smaller caudal scute lies in front of the lower caudal lobe in *Pholidolepis* (*sc*, Text-fig. 4A). Lateral to the posterior ural neural arches, in the apex of the wedge-shaped gap between the proximal part of the uppermost hypaxial fin-ray and the epaxial fulcra, there is in *Pholidolepis* a small patch of thick, rhomboid scales. Four of these thick scales are preserved in P.6067 (*ud 1–4*, Text-fig. 3) and P.44707 (*ud*, Pl. 5, fig. 2), three elongated scales lying in an oblique row, overlapping the uppermost one or two hypaxial fin-rays, and a fourth more rounded scale above them. No specimen shows more than four scales clearly, and the preservation is never sufficiently good to show to what extent these thicker scales were covered by thin, cycloid scales. Like the caudal scutes and the fin-rays, these thickened scales are without enamel. In shape and position these scales correspond with the posterior " urodermals " in several of the specimens figured by Nybelin (1963, *Leptolepis normandica*, text-fig. 10, *Ur 7–8*; *Allothrissops*, text-fig. 11, *Ur 8*; " *Thrissops* " text-fig. 12, *Ur 14–15*; *Eurycormus*, text-figs 13, 15, *Ur*).

In *Pholidophoropsis*, as in *Pholidolepis*, the trunk scales are thin, cycloid, and without enamel. Nybelin (1966 : 415) noted that in *P. caudalis* " some of the posteriormost scales are markedly thicker than the body scales ". In both *P. caudalis* and *P. maculata* there is a very thick, conspicuous caudal scute in front of both the upper and lower lobes of the caudal fin, with a slender anterior process (*ap.sc*, Text-figs 6, 8) which evidently passed down into the musculature. The anterior process and the base of the expanded part of this scale (which is covered by thin, cycloid scales) are without enamel, but the exposed part is enamelled (*e.sc*), like the succeeding epaxial fulcra. This enlarged scale is usually followed by a second median scale, also enamelled (*m.s*, Text-fig. 6) and sometimes (Text-fig. 8A) by a third, before the paired fulcra begin. In *Pholidophoropsis* these epaxial fulcra are very large and conspicuous. On the lateral surface of the posterior ural neural arches and the uppermost hypaxial rays, there is a patch of rhombic, thickened and enamelled scales. Normally there appear to be eight of these scales in both *P. caudalis* (Text-fig. 8B) and *P. maculata*, arranged in an oblique row of five, partially covering the bases of the upper hypaxial rays, with three more rounded scales above them. In the holotype of *P. maculata* (*ud*, Text-fig. 8A) there are ten of these scales, an oblique row of five, an oblique row of four antero-dorsal to these, and a single scale above this (this specimen also shows a row of three or four thick, enamelled scales immediately below the thickened dorsal caudal scute, *d.s*, Text-fig. 8A). In both *P. caudalis* and *P. maculata* the greater part of this patch of thick, rhombic scales is covered by thin, cycloid scales, only the tips of the most posterior scales being exposed (Text-fig. 8).



TEXT-FIG. 8. Sketches of the base of the upper lobe of the tail in *A*, 43055, holotype of *Pholidophoropsis maculata* Nybelin, with ten urodermals; *B*, P.3664*a*, *Pholidophoropsis caudalis* (Woodward), with eight urodermals. The broken lines indicate the posterior limit of the thin, cycloid scales. *b.f*, epaxial basal fulcra; *d.s*, dorsal thickened scales in *P. maculata; f.f*, fringing fulcra; *ms*, median dorsal scales between the caudal scute and the basal fulcra; *sc*, caudal scute; *ud*, urodermals.

III. DISCUSSION

(a) *Comparison with chondrosteans, holosteans and teleosts.*

In Lower Liassic pholidophorids, despite the advanced, almost teleostean condition of the skull (Rayner 1948 : 338; Gardiner 1960 : 347) and other such typically teleostean features as intermuscular bones (Lund 1966), the vertebral column and caudal skeleton retain many strikingly pre-teleostean features. In the vertebral column these primitive features include:

1. Formation of the centra entirely by calcifications in the sheath of the unconstricted notochord. Among actinopterygians centra of this type are known only in the Triassic chondrostean family Pholidopleuridae. In teleosts chordal centra occur as a transient phase in larvae of primitive forms such as *Clupea* (Ramanujam 1929) and *Salmo* (François 1966) and in the Upper Jurassic or Lower Cretaceous *Lycoptera*, sometimes classed as a teleost, sometimes as a halecostome, chordal centra appear to have been present in adults (Saito 1936, pl. 4, fig. 5), although the notochordal calcifications are completely covered by perichordal ossifications.

2. Formation of the centra by opposed, partially or completely separate dorsal and ventral hemicentra. Similar centra are known only in parts of the vertebral column of some pholidopleurids, and in the Triassic chondrostean *Turseodus* (Schaeffer 1967).

3. The diplospondylous structure of the vertebrae in the middle part of the caudal region. This is a typically holostean feature: no teleost or leptolepid is known to show diplospondyly of this type, although all the centra are diplospondylous in young individuals of *Lycoptera* (Saito 1936 : 9) and in the Upper Cretaceous " eel " *Enchelion* (Hay 1903 : 441, pl. 37).

In the caudal skeleton the more important primitive features are:

1. The strong asymmetry of the caudal endoskeleton, with a long, upturned axis, despite the almost perfect external symmetry of the fin.
2. The absence of centra or notochordal calcifications beyond the first ural centrum (except for a series of small, irregular calcifications in *Pholidophoropsis*, Text-fig. 6).
3. The presence of free radials at the tips of the last few haemal spines and the first hypural.
4. The numerous hypurals (11–12).
5. The presence of four (*Pholidophorus bechei*, *Pholidolepis*) or five (*Pholidophoropsis*) epurals.

All these features (except the third, the presence of hypaxial caudal radials, which do not seem to have been found yet in holosteans) are typical of chondrosteans and generalized holosteans: none is found in teleosts[1]. Even in the most primitive teleosts (including the leptolepids) the caudal skeleton is almost symmetrical (although the truncated axis is upturned the hind edges of the hypurals form an almost vertical line), there are two (rarely three, Hollister 1936, Greenwood 1967) perichordally ossified ural centra, eight or fewer hypurals and three or fewer epurals. Teleosts appear to have lost the hypaxial radials[1], not incorporated them into the haemal spines and hypurals. But despite the generally archaic structure of the caudal endoskeleton, these pholidophorids approach or foreshadow the teleosts in the presence of only two lower hypurals which support the majority of the principal rays of the lower caudal lobe (in contrast to amioids (Nybelin 1963, text-figs 17–19) and *Eurycormus* (Nybelin 1963, text-figs 13–15)), in the specialization of the ural neural arches (see below, p. 221), the differentiation of the most posterior scales (both median p. 217, and lateral p. 229), and in the reduction of the number of principal caudal fin-rays in the sequence *Pholidophoropsis* (25–27) – *Pholidophorus bechei* (22–24) – *Pholidolepis* (20–21) towards the generalized teleostean arrangement of 19 principal rays with nine branched in the upper lobe, eight in the lower.

In the earliest leptolepids in which the structure of the vertebral column and caudal skeleton are known (*Leptolepis coryphaenoides* and *L. normandica*, Upper Lias, Rayner 1937, Nybelin 1962, 1963) the vertebrae are perichordally ossified cylinders, constricting the notochord, there is no trace of diplospondyly and the caudal skeleton has the generalized teleostean arrangement of two ural centra, three epurals, no hypaxial radials and about eight hypurals whose hind edges are almost vertical (P.7622, *Leptolepis coryphaenoides*, shows six upper hypurals, 37859, *L. dubia*, shows seven). The structure of the caudal skeleton in Lower Liassic pholidophorids shows that in the pholidophorid/leptolepid transition there was a drastic change in the mode of formation of the centra and a sharp reduction in the asymmetry of the caudal endoskeleton. Possible functional explanations of these changes are discussed below (p. 231).

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[1] Nybelin (pers. commn) has found small ossifications and cartilages at the tips of the last three haemal spines and the first hypural in adult Recent *Elops*. These appear to be much reduced ventral caudal radials, and will be described by Nybelin.

(b) *The homologies of the epurals*

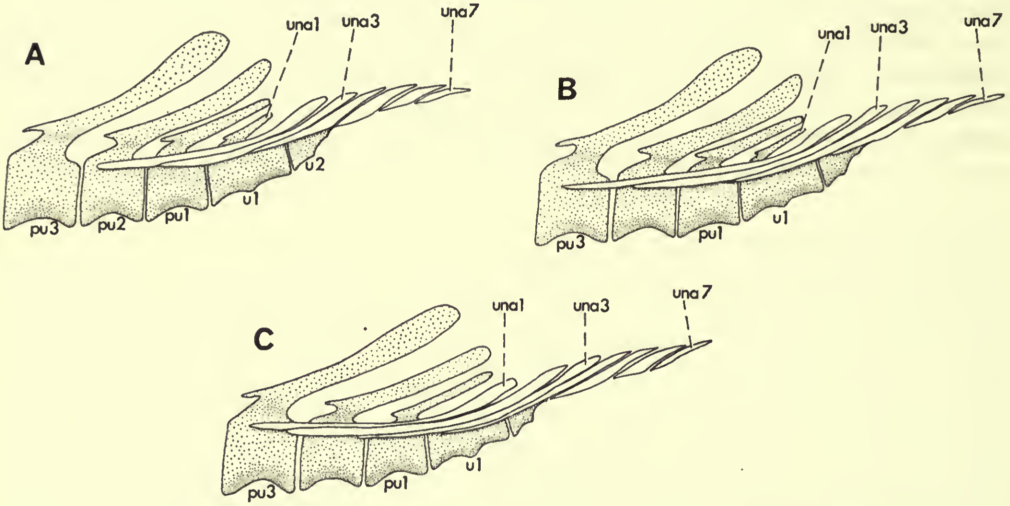
Teleostean epurals, primitively three in number, are normally interpreted as neural spines which have become detached from their neural arches (Gosline 1960, Nybelin 1963, Monod 1967, Greenwood 1967), but they have also been taken to be radials, homologous with the pterygiophores of the dorsal fin (Whitehouse 1910, Goodrich 1930; these authors used the term epural in a different sense from that defined on p. 212). The presence of four epurals in *Pholidophorus bechei* and *Pholidolepis* and five in *Pholidophoropsis* (which is less closely related to the leptolepids and teleosts, p. 236) suggests that the three epurals of generalized teleosts are the remains of a primitively more numerous series. This seems to be confirmed by an examination of more primitive actinopterygians. In the living chondrosteans *Acipenser* (Whitehouse 1910, pl. 47, fig. 2; Schmalhausen 1912, pl. 15, fig. 12) and *Polyodon* (Whitehouse 1910, pl. 47, fig. 3) there is a long series of thirty or more rod-like elements above the posterior neural arches, supporting the epaxial basal fulcra. These cartilages, which are always interpreted as dorsal caudal radials, do not correspond in number or position with the neural arches below them. The only palaeoniscoid in which the caudal skeleton is well known is the Triassic *Pteronisculus* (Nielsen 1942, pl. 24, text-fig. 50), in which there are about fifteen similar elements, also interpreted by Nielsen as dorsal caudal radials, which here have a one-to-one relation to the underlying neural arches. In the Triassic pholidopleurid *Australosomus* (Nielsen 1949, text-fig. 45) there are five dorsal elements, one-to-one above the neural arches. In *Amia* there are three or four dorsal radials (Nybelin 1963, text-fig. 16; Schmalhausen 1912, pl. 18, fig. 56) and in the more primitive amioid *Urocles* there are five (Nybelin 1963, text-fig. 17), in both genera corresponding with the neural arches. Thus there is clear evidence in actinopterygians of a progressive reduction in the number of median dorsal elements below the epaxial basal fulcra (in chondrosteans and most holosteans) or fin-rays (in most teleosts). The epurals of teleosts must be regarded as members of this series of bones, and the name " epural " is sufficiently well established, terse and descriptive to apply to the series in all actinopterygians. There is one-to-one correspondence between the epurals and the neural arches in all the actinopterygians mentioned except *Acipenser* and *Polyodon*: conditions in these two fishes and the fact that in most actinopterygians fulcra or fin-rays articulate with the epurals might suggest that the epurals are dorsal caudal radials, serial homologues of the dorsal pterygiophores, which are primitively not metameric (Lindsey 1956, François 1959). But the articulation between the epurals and the epaxial fulcra or fin-rays is very different from the complex, mobile, muscular joint between dorsal pterygiophores and fin-rays, and in teleosts epaxial fin-rays often articulate with neural spines anterior to the epurals. On the other hand, there is good evidence from several different teleosts that the foremost epural can arise by detachment of a neural spine or can fuse with a neural arch so that it is indistinguishable from a neural spine (Whitehouse 1910, Norden 1961, Patterson, in press, *etc.*): this and the general occurrence, even in palaeoniscoids, of a one-to-one relationship between the epurals and the neural arches indicate that the epurals are detached neural spines, serial homologues of the metameric supraneurals above the anterior neural arches in chondrosteans, most holosteans and many generalized teleosts, which are detached neural spines (Goodrich 1930 : 88; Eaton 1945). If this interpretation is correct, the imperfect correspondence between the epurals and the neural arches in living chondrosteans must be secondary, a reasonable assumption in view of the aberrant nature of the skeleton of these fishes. One is led to the conclusion that the epurals of teleosts are the remains of a longer series of metameric bones in primitive actinopterygians which are detached neural spines, serial homologues of the supraneurals developed anteriorly.

(c) *Uroneurals and urodermals*

On the dorso-lateral surfaces of the ural centra and the first one to four pre-ural centra of primitive teleosts there is a series of paired, elongate bones, extending back between the proximal ends of the epaxial fin-rays. Tate Regan (1910*a*, *b*) named these bones " uroneurals " and interpreted them as " neural arches pertaining to posterior centra which have aborted " (1910*b* : 533). Nybelin (1963) showed that in Upper Jurassic teleosts these bones may be numerous and may extend beyond the axial skeleton on to the surface of the dermal fin-rays, an unlikely position in which to find endoskeletal neural arches. Nybelin compared the series of bones with the elongate rhombic scales covering the body lobe of the heterocercal tail in chondrostean fishes such as *Acipenser*, *Polyodon*, *Birgeria* and *Tarassius*, and interpreted them as scales which have sunk inwards (in phylogeny) and become associated with the vertebral centra, proposing the name " urodermals " for them. The details of the structure of the ural neural arches and the caudal squamation in the pholidophorids described here show that these two interpretations, the endoskeletal " uroneurals " of Tate Regan and the dermal " urodermals " of Nybelin, are not mutually exclusive. The foremost members of the uroneural/urodermal series, normally applied to or fused with the ural and pre-ural centra (the only ones present in the great majority of teleosts), are modified ural neural arches, correctly called uroneurals and referred to as such in the discussion of post-Jurassic teleosts below. The most posterior members of the series, present only in a few primitive teleosts and lying on the uppermost hypaxial fin-rays, are scales, almost unmodified relics of the thick, rhombic scales of *Pholidophorus*, and are correctly called urodermals.

(i) *The uroneurals.*

In *Pholidophorus bechei* (Pl. 1, Pl. 3, fig. 1, Pl. 5, fig. 1; Text-figs 1, 2, 5), *Pholidolepis* (Pl. 2, Pl. 3, fig. 2; Text-figs 3, 4) and *Pholidophoropsis* (Pl. 4; Text-fig. 6) the ural neural arches are paired structures and those behind the first are successively modified into elongate, rod-like structures, each fitting closely into a hollow on the antero-dorsal surface of its successor. In *Pholidophorus bechei* there are seven or eight pairs of ural neural arches, in *Pholidophoropsis maculata* there are eight, and in both species all but the first two pairs are modified, elongate structures. In *Pholidolepis* only seven pairs of ural neural arches have been seen, all but the first pair modified. Since these bones are in series with and grade into the pre-ural neural arches, lie directly over the space occupied in life by the notochord, are thick and consist internally of cancellous endochondral bone, and in *P. bechei* are completely covered by thick, enamelled scales, there can be no doubt that they are endoskeletal neural arches, not dermal scales.



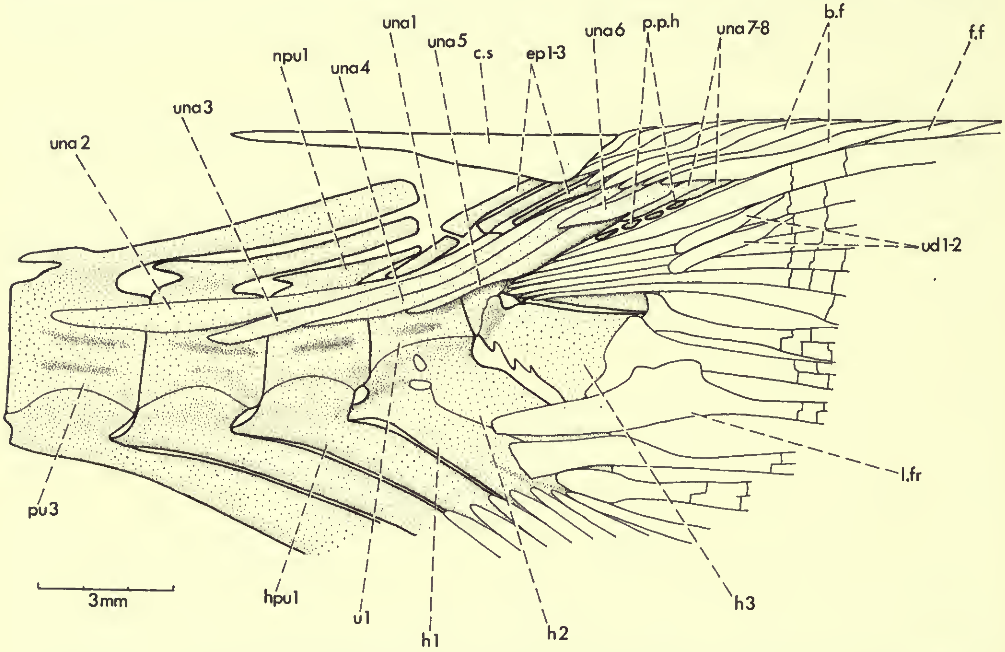
Text-fig. 9. Sketches illustrating variations in the ural neural arches in *Leptolepis coryphaenoides*. In *A* and *B* the first ural neural arch is unmodified, in *C* it is modified into a uroneural. In *A* the first uroneural extends to the second pre-ural centrum, in *B* to the third. *pu 1–3*, pre-ural centra; *u 1*, *u 2*, ural centra; *una 1*, *una 3*, *una 7*, ural neural arches 1–7.

The seven or eight ural neural arches of Lower Liassic pholidophorids may be compared directly with the uroneurals of the Upper Liassic *Leptolepis coryphaenoides* and *L. normandica* (Text-fig. 9; Nybelin 1963, text-figs 9, 10). In P.948 (*L. coryphaenoides*, Nybelin 1963, text-fig. 9) the first ural neural arch is unmodified, as in pholidophorids, and there are six modified ural neural arches (*una 2–7*, Text-fig. 9; *Ur 2–7* in Nybelin's figure). *Ur 8*, the most posterior element labelled in Nybelin's figure, is probably not a ural neural arch but the remnant of the uppermost hypaxial fin-ray, already much reduced in *Pholidophorus* and *Pholidolepis* (*r.fr*, Text-figs 1, 3, 7). In contrast to *Pholidolepis*, where the fourth ural neural arch is the longest and none of the ural neural arches extends forwards beyond the first ural centrum, in *L. coryphaenoides* the second to fourth ural neural arches are equally long, the second extending forwards to the second (Text-fig. 9A) or third (32456, Text-fig. 9B) pre-ural centrum, the third to the first or second pre-ural centrum, and the fourth to the first ural centrum (which in *Leptolepis* and all teleosts supports the first two hypurals and is the product of fusion of two centra). A further variation found in both *L. coryphaenoides* (32467, Text-fig. 9C) and *L. normandica* (32583) is that the first ural neural arch, unmodified in pholidophorids and in most specimens of these two species, is elongated like its successors, extending forwards to the third pre-ural centrum. *Leptolepis normandica* does not seem to differ from *L. coryphaenoides* in the structure of the ural neural arches, but some of the specimens identified as *L. coryphaenoides* may be *L. normandica* since the two species are at present distinguishable only when the head is well preserved.

In the more advanced Upper Jurassic form *Allothrissops* (P.915, P.917*a*, P.3680*c*, P.7663; Nybelin 1963, text-fig. 11, Patterson 1967, text-fig. 3) one can recognize seven ural neural arches, the first unmodified, the second to seventh all greatly elongated and sometimes showing fusions (Patterson 1967, text-fig. 3, D 5+6) or apparent subdivisions (Nybelin 1963, text-fig. 11, *Ur 6–7*). As in some specimens of *Leptolepis coryphaenoides*, the second ural neural arch extends forwards to the third pre-ural centrum, but in contrast to *L. coryphaenoides* the third, fourth, and often the fifth extend to the second pre-ural centrum, the sixth extends to the first pre-ural centrum and the seventh to the first ural centrum. In the related Upper Jurassic *Thrissops* (P.3684; Nybelin 1963, text-fig. 12) the ural neural arches are as in *Allothrissops* except that the second is even more elongate, extending forwards to the fourth pre-ural centrum, and in Nybelin's figured specimen there are seven elongate ural neural arches (*Ur 1–7*).

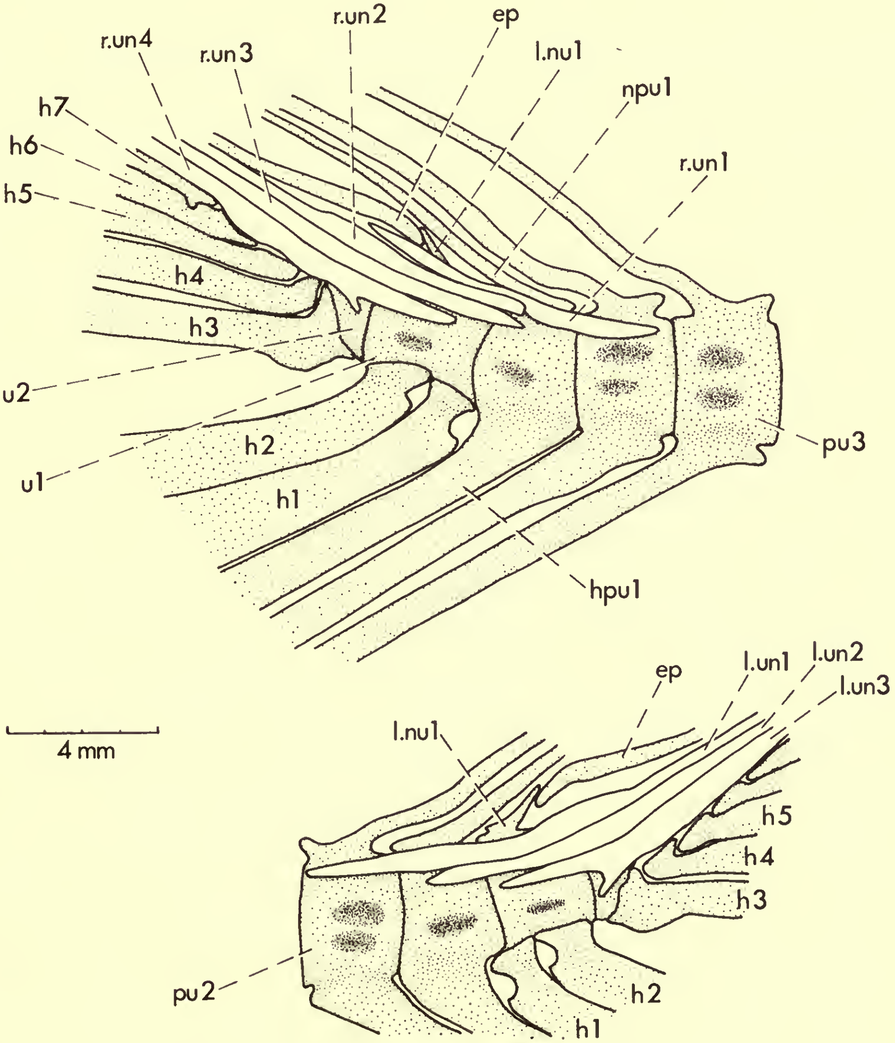
In the Upper Jurassic *Leptolepis dubia* (Text-fig. 10; Nybelin 1963, text-fig. 8, Patterson 1967, text-fig. 6), in which the skull is in many ways more primitive than in *Allothrissops* (Patterson 1967, text-figs 2, 4), the condition of the ural neural arches is more complex. The first five ural neural arches do not differ from those of *Allothrissops* and *Leptolepis coryphaenoides*; the first (*una 1*) is unmodified and the second to fifth (*una 2–5*) are greatly elongated, the second extending forwards to the third pre-ural centrum (*pu 3*). Behind the fifth ural neural arch there are three less elongate bones (*una 6–8*), the first originating well behind the second ural centrum, which are inclined in sequence behind one another as are the preceding ural neural arches, but which lie *lateral* to the fifth ural neural arch. This arrangement can be seen in several specimens (37090, 37847, 37859, 37865; Nybelin 1963, text-fig. 8, *Ur 5–7*, Patterson 1967, text-fig. 6, *D 5–7*) and seems to be constant for the species. In shape and in their mode of articulation with each other (best seen in 37090) these three posterior bones resemble the posterior ural neural arches of pholidophorids and *Leptolepis coryphaenoides*, and like them they end posteriorly *medial* to the bases of the epaxial basal fulcra (*b.f.*). Since these three bones correspond in number and position with the sixth to eighth ural neural arches in pholidophorids they are clearly ural neural arches, despite their differentiation from the more anterior arches and their position lateral to the fifth.

Among known Cretaceous and later teleosts the maximum number of elongate, strap-shaped uroneurals (ural neural arches) is five, which occurs in some specimens of the Upper Cretaceous genera *Xiphactinus*, *Ichthyodectes* and *Gillicus* (Cavender 1966): in some specimens of *Xiphactinus* there are four long uroneurals on one side, five on the other (Cavender 1966 : 6). These Cretaceous ichthyodectids also show the maximum forward extension of the uroneurals, which may reach the fourth pre-ural centrum, as in *Thrissops*. Among living teleosts the maximum number of elongate uroneurals is four, found in some specimens of *Hiodon* (Gosline 1960 : 341). The specimen of *Hiodon alosoides* figured by Gosline (BMNH 1892.12.30.555; 1960, text-fig. 4) shows a most interesting condition. On the left side of the tail (Text-fig. 11) there are three long uroneurals (*l.un 1–3*), the first ending anteriorly on the second pre-ural centrum (*pu 2*), the second and third on the first pre-ural and first ural centra respectively. The third uroneural has a small ventral process on the second ural centrum (*u 2*): this process (present on both sides of the specimen) probably indicates that the third uroneural is a compound structure formed by fusion of two ural neural arches, almost certainly homologous with the fourth and fifth ural neural arches of *Leptolepis*. On the right side of this specimen of *Hiodon alosoides* (Text-fig. 11) there are four uroneurals, as Gosline (1960 : 341) noted, but the first of these (*r.un 1*), ending anteriorly on the second pre-ural centrum, is short



Text-fig. 10. The caudal skeleton of *Leptolepis dubia*, drawn mainly from P.927, slightly restored. *b.f*, epaxial basal fulcra; *c.s*, caudal scute; *ep 1–3*, epurals; *f.f*, fringing fulcra; *h 1–3*, hypurals 1–3; *hpu 1*, first pre-ural haemal spine; *l.fr*, expanded base of lowermost fin-ray of upper caudal lobe; *npu 1*, first pre-ural neural arch; *p.p.h*, postero-dorsal processes on heads of upper hypurals; *pu 3*, third pre-ural centrum; *u 1*, first ural centrum; *ud 1–2*, urodermals; *una 1–8*, first–eighth ural neural arches.

and is continuous posteriorly with the small neural arch on the first ural centrum (the first ural neural arch), a structure which is unmodified on the left side of the specimen (*l.nu 1*), and in all the fishes so far discussed except some individuals of *Leptolepis coryphaenoides* and *L. normandica* (Text-fig. 9C). The second uroneural (*r.un 2*), the antimere of the first on the left side of the fish and representing the second ural neural arch, is truncated anteriorly and ends on the first pre-ural centrum,


r.un4
r.un3
r.un2
ep
l.nu1
npu1
r.un1
h7
h6
h5
h4
h3
u2
h2
u1
h1
pu3
hpu1
4 mm
ep
l.un1
l.un2
l.un3
l.nu1
h5
h4
h3
pu2
h2
h1

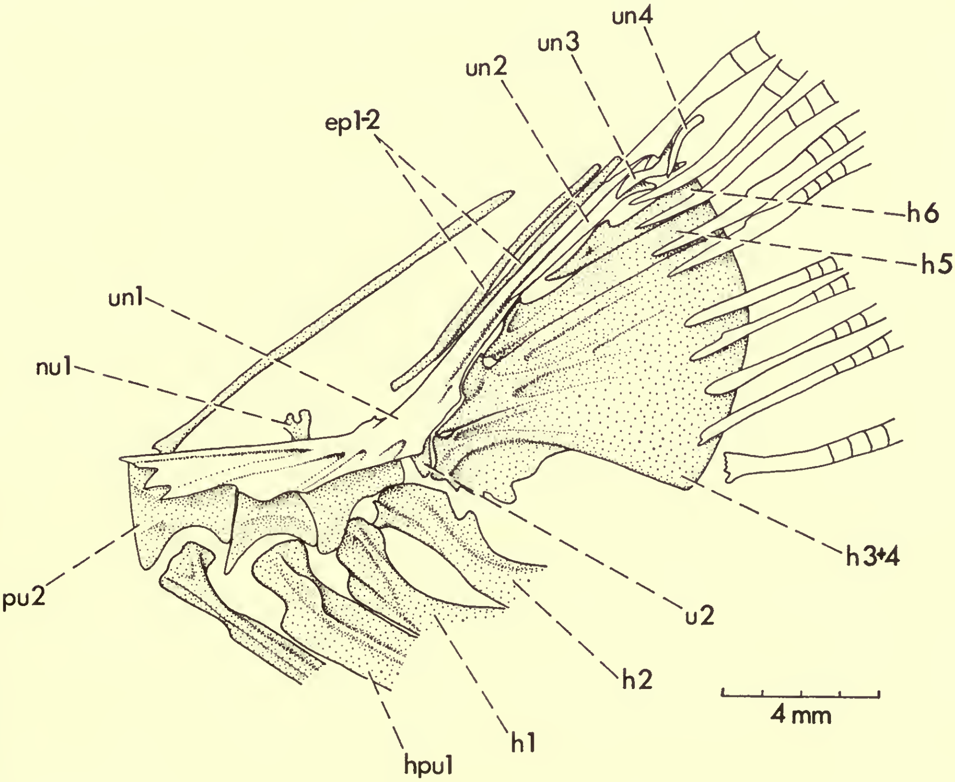
TEXT-FIG. 11. *Hiodon alosoides*, caudal skeleton of BMNH 1892.12.30.555, right side above, left side below. *ep*, epural; *h 1–7*, hypurals; *hpu 1*, haemal spine of first pre-ural vertebra; *l.nu 1*, first ural neural arch of left side; *l.un 1–3*, uroneurals of left side; *npu 1*, neural spine of first pre-ural vertebra; *pu 2*, *pu 3*, second and third pre-ural centra; *r.un. 1–4*, uroneurals of right side; *u 1*, *u 2*, first and second ural centra.

above the tip of the third uroneural (*r.un 3*). The individual abnormality on the right side of this specimen of *Hiodon alosoides* shows beyond question that uroneurals arise by modification of ural neural arches, and indicates that the morphogenetic mechanism inducing these modifications may occasionally operate beyond its usual field (the second and more posterior ural neural arches). The five uroneurals which Cavender (1966) found in some specimens of the Cretaceous *Xiphactinus*, *Ichthyodectes* and *Gillicus* may be the result of a similar modification of the first ural neural arch, for Cavender found no neural arch on the first ural centrum in these fishes, and the first uroneural in the specimen of *Ichthyodectes* which he figures (text-fig. 1A) is very like the modified first ural neural arch of *Hiodon* in size and length. This unusual plasticity of the ural neural arches in ichthyodectids and *Hiodon* (which probably belong to the same teleost lineage, Greenwood *et al.* 1966 : 360) is interesting in view of the complete loss of uroneurals in most osteoglossomorph teleosts (Greenwood 1967).

In the primitive living teleosts *Elops*, *Megalops* and *Tarpon* there are three uroneurals (Tate Regan 1910*a*, text-fig. 1; Hollister 1936, text-figs 14, 16, 19; Nybelin 1963, text-figs 4, 7, *Ur 1–3*). The first two are elongated bones ending anteriorly on the second (*Elops*) or first (*Megalops*, *Tarpon*) pre-ural and the first ural centrum respectively, the third a small splint originating well behind the second ural centrum and lying below (*Megalops*, *Tarpon*) or lateral (*Elops*) to the tip of the second. In *Elops* the anterior end of the first uroneural is forked, the upper limb passing forwards to the second pre-ural centrum, the lower ending on the first pre-ural. Tate Regan (1910*a*) considered this forking to indicate that the first uroneural is a compound bone, and saw a line of junction between the two components in some specimens. Although neither Hollister (1936) nor Nybelin (1963) saw such a line, this is probably true: in the dussumieriid *Jenkinsia* the first uroneural corresponds in position with that of *Elops* and arises as two bones which later fuse (Hollister 1936 : 279). Exactly similar forking of the first uroneural is seen in other teleosts (“ *Clupavus* , Patterson 1967, text-fig. 11; *Nematonotus*, Patterson, in press, text-fig. 25) and probably always indicates that two ural neural arches have fused. Tate Regan also saw a line of junction in the second uroneural of *Elops*: if this observation were confirmed this uroneural would correspond with the compound third uroneural of normal individuals of *Hiodon* (Text-fig. 11), which it resembles in size and position, just as the compound first uroneural of *Elops* corresponds to the first two uroneurals of normal *Hiodon*, and the two large uroneurals of *Elops* would be homologous with the second to fifth ural neural arches of *Leptolepis*. The small third uroneural of *Elops*, *Megalops* and *Tarpon*, originating behind the second ural centrum, lying lateral to or behind the tip of the second (= 4th + 5th ural neural arches) and ending medial to the bases of the fin-rays, has no homologue in *Hiodon* but exactly resembles the sixth ural neural arch of *Leptolepis dubia* (*una 6*, Text-fig. 10) and a similarly placed third uroneural in many teleosts (young *Albula*, Hollister 1936, text-fig. 23; clupeoids, Hollister 1936, text-figs 43–52, Cavender 1966, text-figs 3, 4, Monod 1967, text-fig. 9, Patterson 1967*a*, text-fig. 8; salmonids, Schmalhausen 1912, pl. 18, fig. 60, Norden 1961, pls. 14, 15, Gosline 1960, text-figs 5, 12; *Argentina*, Gosline 1960, text-fig. 10; non-siluroid ostariophysans, Weitzman

1962, text-fig. 15, Gosline 1961, text-fig. 1D). Occasionally there is a second small uroneural, as in the specimen of *Salvelinus grayi* figured by Gosline (1960, text-fig. 2, UN 4). In this specimen (BMNH 1905.12.8.5) the small fourth uroneural is comparable to the seventh ural neural arch of *Leptolepis dubia* (*una 7*, Text-fig. 10), but a similar structure has not been found in other individuals of this species, or in other salmonids, although the caudal skeleton of these fishes has received more attention than that of any other group (Norden 1961, Vladykov 1962, and many ealier papers).

In a specimen of *Alepocephalus rostratus*, Gosline (1960, text-fig. 1) shows two small uroneurals (UN 2, 3) comparable with the third and fourth uroneurals in *Salvelinus grayi*, but in this specimen (BMNH 1886.8.4.7; Text-fig. 12) I find a small fourth uroneural (*un 4*) which is separate only on the left side of the fish, being fused into the third uroneural on the right side. This individual of *Alepocephalus* has three small uroneurals (*un 2–4*) comparable with the sixth to eighth ural neural arches in *Leptolepis dubia* (*una 6–8*, Text-fig. 10). The first uroneural in *Alepo-*



Text-fig. 12. *Alepocephalus rostratus*, caudal skeleton of BMNH 1886.8.4.7. The neural arch of the first pre-ural centrum is broken off in this specimen. *ep 1–2*, epurals; *h 1–6*, hypurals; *hpu 1*, haemal spine of first pre-ural vertebra; *nu 1*, first ural neural arch; *pu 2*, second pre-ural centrum; *u 2*, second ural centrum; *un 1–4*, uroneurals.

cephalus (*un 1*) is very large and appears to consist of four fused ural neural arches, two ending anteriorly on the second pre-ural centrum (*pu 2*), and one ending at the hind end of both the first pre-ural and the first ural centra. This fish also has a small unmodified and paired neural arch on the first ural centrum (*nu 1*, the first ural neural arch), and an indication of the posterior end of the second ural neural arch in a process on the upper edge of the first uroneural above the hind end of the first ural centrum. *Alepocephalus* seems to exhibit the most complete set of uroneurals among living teleosts, with traces of eight ural neural arches, the first (*nu 1*) unmodified, the second to fifth much elongated and fused (*un 1*), the sixth to eighth small and separate (*un 2–4*).

Interpretation of the uroneurals of teleosts as modified ural neural arches is supported by Monod's observation (1967) that in elopoids the uroneurals may be preformed in cartilage. But it is necessary to account for two features of the uroneurals which have been taken to indicate that they are of dermal origin, the fact that they normally ossify without cartilage precursors, even in such primitive fishes as *Megalops* (Hollister 1939, text-fig. 16, Nybelin 1963 : 514) and *Clupea* (Ramanujam 1929 : 396), and the superficial appearance of the uroneurals in adult fishes, where they are usually easily differentiated from the preceding neural arches by their smooth, dense texture, suggesting dermal bone (Greenwood 1967). In pholidophorids it has been noted (p. 212) that the lateral surfaces of the ural neural arches are smooth, dense and glossy, but this is also true of the postero-dorsal processes on the heads of the upper hypurals (p. 210). The explanation of these points is probably to be found in the progressive replacement of endochondral and perichondral bone by membrane bone which occurs in the evolution of the vertebral column of teleosts. In primitive teleosts the neural and haemal arches are formed largely by ossification of cartilage, but in advanced teleosts the amount of cartilage is greatly reduced and the arches may consist entirely of membrane bone (François 1966 : 319). In *Clupea* the neural and haemal arches of the trunk ossify perichondrally and endochondrally, but the uroneurals ossify as membrane bones at a very early stage (2–2·5 cm., Ramanujam 1929 : 391). The precocious ossification of the uroneurals in ontogeny (which must occur for functional reasons) is apparently accompanied by a precocious replacement of endochondral bone by membrane bone in phylogeny, and it is this different mode of ossification which accounts for the dense texture of the uroneurals.

The history of the uroneurals in teleosts may be summarized as follows:

1. The uroneurals arose by modification of the second and more posterior members of the series of seven or eight pairs of ural neural arches present in pholidophorids, and are therefore primitively six or seven in number. Occasionally the first ural neural arch is also modified (*Leptolepis*, *Hiodon*, ? ichthyodectids).

2. There are six separate uroneurals in *Leptolepis coryphaenoides* (Text-fig. 9) and *L. normandica* (Lower Jurassic) and six or seven in *L. dubia* (Text-fig. 10), *Allothrissops* and *Thrissops* (Upper Jurassic). In post-Jurassic teleosts the number of uroneurals is reduced by loss or by fusion between members of the series.

3. The seven uroneurals of *Leptolepis dubia* are differentiated into an anterior set of four elongated, strap-like bones (representing the second to fifth ural neural arches)

and a posterior set of three short bones (ural neural arches 6–8) which originate well behind the second ural centrum and lie lateral to the anterior uroneurals. These two sets of uroneurals are recognizable in primitive members of all the major basal groups of teleosts (Elopomorpha, Clupeomorpha, Protacanthopterygii, Ostariophysi) except the Osteoglossomorpha (ichthyodectids and *Hiodon* (Text-fig. 11)), which have elongate uroneurals only: this supports the view that the Osteoglossomorpha are derived from near *Thrissops* and *Allothrissops*, in which the uroneurals are still all of one type.

4. The anterior set of four elongate uroneurals, one of which normally ends anteriorly on each of the first two pre-ural and the two ural centra, is complete only in the Cretaceous ichthyodectids (Cavender 1966) among post-Jurassic teleosts. In Upper Cretaceous " *Clupavus* " the first and second of the four are fused (Patterson 1967, text-fig. 11), in *Hiodon* the third and fourth are fused (Text-fig. 11), and in *Elops* both the first and second and the third and fourth are fused to produce two large uroneurals. Similar fusions to those in *Elops* are probably responsible for the two large uroneurals of clupeomorph, protacanthopterygian and ostariophysan fishes, and these are the only uroneurals to persist above the myctophoid level.

5. Fusions between these large anterior uroneurals and centra are common in teleosts. Usually the fusion is between the first uroneural (itself probably compound) and a compound centrum formed by fusion of the first ural and pre-ural centra: this occurs notably in clupeoids, ostariophysans, gonorynchiforms, atherinomorphs and in many paracanthopterygians and acanthopterygians.

6. A second type of fusion, especially characteristic of many protacanthopterygian and acanthopterygian groups, is the incorporation of the first ural neural arch, and usually also of the first pre-ural neural arch, into the first uroneural to produce the " stegural " of Monod (1967).

7. The posterior set of uroneurals consists primitively of three small, splint-like bones lying lateral to or behind the tip of the last elongate uroneural and ending posteriorly medial to the bases of the epaxial fin-rays. These bones represent the sixth to eighth ural neural arches of pholidophorids and *Leptolepis dubia*. Excepting *Alepocephalus* and a single specimen of *Salvelinus grayi*, I know of no post-Jurassic teleost which has more than one of these small uroneurals. *Alepocephalus* (Text-fig. 12) has three, the specimen of *Salvelinus grayi* has two. A single posterior uroneural is present in elopoids, clupeoids, many protacanthopterygians and non-siluroid ostariophysans: whether this bone is compound in origin is as yet unknown.

8. Replacement of endochondral and perichondral bone by membrane bone, which occurs in the neural and haemal arches during the evolution of teleosts, took place precociously in the uroneurals, so that they are normally ossified without cartilage precursors and differ in texture from the preceding neural arches.

(ii) *The urodermals*

In *Pholidophoropsis* and *Pholidolepis*, although the trunk scales have become thin, cycloid and have lost their enamel, there remains a small patch of thick, rhombic scales, enamelled in *Pholidophoropsis*, in the apex of the much reduced body lobe of the caudal fin (Pl. 5, fig. 2; Text-fig. 8). These scales cover the last few ural neural arches and parts of the bases of the upper hypaxial fin-rays. In *Pholidophoropsis* there are eight to ten of these scales, in *Pholidolepis* there are four. In *Leptolepis dubia* two slender, horizontally elongate bones lie one above the other lateral to the bases of the upper hypaxial fin-rays (Text-fig. 10, *ud 1–2*; Nybelin 1963, text-fig. 8, *Ur 8–9*; Patterson 1967, text-fig. 6, *D* 8–9), and two exactly similar bones are also present in *L. coryphaenoides* (32463, 32467, P.7622) and *L. normandica* (32583; Nybelin 1963, text-fig. 10, *Ur 7–8*). As Nybelin showed, since these bones are superficial to dermal fin-rays they must be dermal in origin: they are obviously homologous with the four thickened scales in this position in *Pholidolepis*, and Nybelin's term " urodermals " should be used for them. In *Leptolepis* there is no evidence of the presence of more than two urodermals. In *Allothrissops* there is normally a single urodermal (Nybelin 1963, text-fig. 11, *Ur 8*; Patterson 1967, text-fig. 3, *D* 8), but P.917*a* has two, similar in shape and position to those of *Leptolepis*. In the " *Thrissops* " specimen figured by Nybelin (1963, text-fig. 12) there are two urodermals (*Ur 14–15*), as in *Leptolepis*: in front of these, below the last elongate uroneurals, there is a row of five elongate-rhombic bones (*Ur 9–13*). These five bones do not appear to be urodermals (scales) since they are arranged in a pattern which is a dorso-ventral mirror image of the normal scale pattern on the tail (cf. text-figs. 2, 3, 15, 18 in Nybelin's paper). In *Leptolepis dubia* and *Allothrissops* I have figured a row of small bones in a similar position (Patterson 1967, text-fig. 3, D 9–11, text-fig. 6, D 10–12), but I now believe that these are postero-dorsally directed knobs on the upper hypurals, like those in pholidophorids (*p.p.h*, Text-figs 1–3, 10). The five bones in Nybelin's " *Thrissops* " specimen appear too large to be knobs on the upper hypurals and at present I am unable to interpret them. Apart from this one specimen, no Jurassic teleost is known to have more than two urodermals.

The history of the urodermals in post-Jurassic teleosts can be described briefly. The only post-Jurassic teleosts in which urodermals have been figured are the living *Elops* (Hollister 1936, text-fig. 14; Nybelin 1963, text-figs 4, 5, *Ur 4*) and Upper Cretaceous " *Clupavus* " (Patterson 1967, text-fig. 11, D6) and *Nematonotus* (Patterson, in press, text-fig. 25): in all there is only a single urodermal, lying on the fin-rays, well clear of the uroneurals. In *Elops* the single urodermal is slender and elongate, resembling those of *Leptolepis*, in " *Clupavus* " and *Nematonotus* it is shorter and more ovoid. A single ovoid urodermal also occurs in the Upper Cretaceous myctophoid *Sardinioides attenuatus* and in the living *Coregonus* and *Osmerus* (Nybelin, pers. commn) and *Argentina*. No doubt a single urodermal was present in other Cretaceous teleosts, but it will only be visible in exceptionally well preserved specimens and I have not seen one in a cursory examination of likely genera. Probably a urodermal occurs in other primitive living teleosts, perhaps in a reduced form, but again I have not found one in a brief search. In teleosts urodermals are evidently vestigial structures, retained from pholidophoroid ancestors; like other such structures (gular, pectoral and pelvic splints, caudal scutes, fringing fulcra on the upper caudal lobe, etc.), they are of limited occurrence and no obvious functional significance.

Differentiation of the scales at the tip of the reduced axial lobe of the tail from the trunk scales to produce urodermals is not confined to the pholidophoroid/teleost lineage; it also occurred in amioid holosteans (Nybelin 1963, text-figs 17–20).

(iii) *The function of the uroneurals*

It is necessary to consider why the ural neural arches should have become so remarkably modified in the evolution of teleosts. Tate Regan (1910*a*) wrote that the uroneurals " have taken on the function of strengthening the upturned vertebrae, thus replacing and inducing the abortion of the posterior centra ". Nybelin (1963) also found the uroneurals to have a strengthening function since in Jurassic forms they were best developed in fishes with a slender caudal peduncle and a large, deeply forked caudal fin. Nybelin's comparison of the uroneurals with the scale rows of the body lobe of the tail in chondrosteans is important. The scales of the caudal axis in chondrosteans are separated from those of the trunk by a more or less sharp oblique line at which the orientation of the scale rows changes from antero-dorsal–postero-ventral on the trunk to antero-ventral—postero-dorsal on the tail. That this is a real change in orientation of the scales is shown by the reversed direction of the overlapping of the scales and of the keels and peg-and-socket joints on the inner surface of the caudal scales (Schultze 1966 : 255, text-fig. 11*b*). Smith (1956 : 12) noted that this line is a functional boundary, " a hinge about which bending moments occur ". The strong fibrous attachments between the scales in each caudal scale row which Smith (1956) described in sturgeons link the rows into functional units. Smith considered the role of the caudal scale rows to be primarily protective, but it seems much more probable that they serve to stiffen the upper lobe of the tail: this may give the upper lobe less flexibility than the lower, so that the tail will generate lift even when it is externally symmetrical (Affleck 1950), as it is in *Polyodon* and many fossil chondrosteans, or it may serve simply to equalize the flexibility of the two lobes, since the lower lobe should be basically more rigid than the upper because of the direct alignment of the lepidotrichia and the supporting haemal spines. As Smith noted, the functional value of the caudal squamation in chondrosteans is indicated by the retention of these scales in many chondrosteans which have lost or greatly reduced the trunk squamation (sturgeons, *Polyodon*, *Carboveles*, *Coccolepis*, *Dorypterus*, *Birgeria*, etc.).

It is well known that the evolution of the tail in actinopterygians is linked with buoyancy and swimming efficiency (see especially Alexander 1966). The reduction in ossification and thinning of the scales characteristic of many actinopterygian lineages together with the possession of a swim-bladder lead to a reduction in specific gravity and the attainment of neutral buoyancy, which allows a great saving in energy previously expended in generating lift (Alexander 1966, table 1). In the tail the principal change involved is the gradual reduction of the body lobe of the lift-generating (epibatic, Affleck 1950) heterocercal tail towards the isobatic homocercal tail of teleosts. In pholidophorids the body lobe of the tail is greatly reduced and the fin is externally almost perfectly symmetrical (Text-fig. 7), but the endoskeleton and the arrangement of the bases of the fin-rays (Text-figs 1–4) are still strongly asymmetrical. The primitive stiffeners of the caudal axis, the scales of the body lobe, have been lost and replaced by two new sets of stiffeners, the ural neural arches (above or lateral to the notochord) and the fin-rays (below the notochord). In chondrosteans the upper hypaxial fin-rays are short, inserting on the underside of the long body lobe of the tail. In pholidophorids it appears that as the body lobe has been reduced the upper hypaxial fin-rays are elongated to retain their insertion, the long bases of these rays eventually replacing the caudal scales as stiffeners of the caudal axis. The seven or eight upper hypaxial rays of pholidophorids are very deeply cleft basally and cross the upper hypurals almost at right angles, ending on the third or fourth hypural. On the heads of most of the upper hypurals there are peg-like postero-dorsal processes which fit against the uppermost fin-ray (*p.p.h*, Text-figs 1–3) and were presumably bound to the fin-rays by connective tissue, locking them in position. This arrangement, a bundle of thin, slightly flexible rods (the bases of the fin-rays) bound to both surfaces of a row of stout rods (the hypurals) lying at right angles to them, must have been rather rigid. The ural neural arches of pholidophorids, though considerably modified (Text-fig. 5) and interlocking with each other to form a semi-rigid rod, were applied to an uncalcified notochord and did not extend forwards to gain support from the calcified part of the notochord: probably they were less effective stiffeners than the fin-ray/hypural system. It is important to note that both sets of stiffeners, the fin-rays and the ural neural arches, end at about the same level, the second ural segment (second hypural and second ural neural arch), an oblique plane of weakness which is emphasized by the termination of the first three pre-ural neural spines and the origin of the epurals in the same plane (Text-figs 1, 3, 4.). This plane of weakness corresponds with the functional boundary (hinge) at which the scales change their orientation in palaeoniscoids and at which the caudal squamation ends in such forms as *Polyodon* (Nybelin 1963, text-fig. 3), sturgeons (Smith 1956, text-fig. 1), *Birgeria* (Nielsen 1949, text-fig. 77), *Coccolepis*, *etc.*

In teleosts this " hinge " at the base of the upper caudal lobe has disappeared. There are two well ossified ural centra to which the uroneurals are closely applied and the uroneurals have extended forwards across the level of the " hinge " to gain support from the first two or three pre-ural centra (Text-figs 9–12), forming a highly effective set of stiffeners braced on the vertebral column. The upper principal fin-rays in Jurassic teleosts (*Leptolepis*, *Allothrissops*, *Thrissops*; Text-fig. 10; Nybelin 1963, text-figs. 8–12) have deeply cleft bases which cover the upper hypurals, as in pholidophorids, but the angle between the axes of the fin-rays and the hypurals is much smaller and the differentiation between the upper and lower principal rays in the degree of overlap on the hypurals is less: in these early teleosts the uroneurals can be seen to be replacing the fin-ray/hypural system as the main brace of the upper lobe of the tail. In Cretaceous and later teleosts the upper and lower fin-rays are normally symmetrically arranged (either both upper and lower principal fin-rays are deeply cleft at the base, as in scombrids and carangids, or neither is deeply cleft) and dorso-ventral symmetry is increased by conversion of the epaxial basal fulcra into segmented fin-rays (Tate Regan 1910*a* : 357). Even in such a primitive teleost as *Elops* the arrangement of the fin-rays shows almost perfect dorso-ventral symmetry and the upper principal rays are directly aligned with their supporting hypurals (Nybelin 1963, text-fig. 4). The uroneurals here appear to strengthen the weak supports of the upper caudal lobe (several small hypurals articulating with a small centrum or with the uncalcified notochord, Nybelin 1963, text-fig. 1) so that the two lobes of the fin will be equally flexible, and the pre-ural neural spines have increased in length, crossing the line of the " chondrostean hinge " to give added rigidity and symmetry.

These facts suggest that the tails of pholidophorids and teleosts functioned in rather different ways. In pholidophorids the body lobe is much reduced, the fin is externally symmetrical and the chondrostean system of stiffening the upper lobe by scales is obsolete, but the endoskeleton is still basically chondrostean and there was an oblique plane of weakness at the level of the second ural neural arch, both sets of stiffeners, the fin-rays and the ural neural arches, ending at this point, and the junction between the pre-ural neural spines and the epurals lying in the same plane. This plane of weakness, indicating a line of flexion, corresponds with the line of flexion in the scaling of chondrostean tails, and the musculature and mode of operation of the pholidophorid tail must have been similar to those of chondrosteans, with a stiff upper lobe swinging about an oblique axis. In teleosts, ossification of the ural and pre-ural centra and forward extension of the uroneurals have eliminated the chondrostean line of flexion. The uroneurals equalize the flexibility of the upper and lower lobes of the fin and the fin-rays lose their stiffening function and soon become symmetrically arranged. The endoskeleton is also almost symmetrical even in primitive teleosts. These changes are presumably associated with the advantages of neutral buoyancy, but it is difficult to believe that neutral buoyancy was attained only at the teleost level—a fish like *Pholidolepis* which must have had a swimbladder, had the scales reduced to the typical teleost form, and swam in sea water (specific gravity 1·025) was certainly capable of achieving neutral buoyancy. Even in *Pholidophorus*, where the scales are still thick, rhombic and enamelled, neutral buoyancy was surely attainable in view of Alexander's observation (1966 : 145) that *Lepisosteus*, with very heavily ossified scales and freshwater habitat, can remain motionless in mid-water. The advantages which the teleosts had over the pholidophorids are probably due not to the sudden acquisition of neutral buoyancy but to three factors, the advantage in the reduced rate of change of buoyancy with depth which accrues to a fish with a low specific gravity and a small swimbladder (Alexander 1966 : 148), the increased efficiency in horizontal swimming of a fish in which both lobes of the tail are equal in area and in flexibility, in which the axis is not upturned, and in which the tail swings about a vertical rather than an oblique axis (Affleck 1950), and the greater flexibility and elasticity of a trunk which contains a well ossified vertebral column and is covered by thin, flexible scales.

Returning to the question posed at the beginning of this section, why should the ural neural arches have become so remarkably modified in teleosts, I conclude that both Tate Regan and Nybelin were correct in interpreting the uroneurals as stiffeners, but that the most remarkable feature of the uroneurals, their extension forwards to articulate with or fuse with centra well in front of the segments in which they originally arose, is a method of eliminating the " chondrostean hinge ", producing a tail which swings about a vertical axis and is then free to develop internal symmetry. Tate Regan's opinion that the uroneurals " replace and induce the abortion of the posterior centra " is not strictly correct, for in phylogeny these posterior centra never existed. The uroneurals developed before the ossification of the centra, and by their presence made numerous ural centra unnecessary. In amioid holosteans, where the endoskeleton of the tail remains strongly asymmetrical, uroneurals did not develop but the " chondrostean hinge " was eliminated by the development of many ural centra extending to the tip of the notochord (Nybelin 1963, text-figs 16, 17, 19). Although amioids attained neutral buoyancy, this method of stiffening the caudal axis has prevented them from developing a fully efficient internally symmetrical tail.

(d) *Definition of the Teleostei*

In a discussion of possible taxonomic definitions of the Teleostei (Patterson 1967) I reached the conclusion that the caudal skeleton provides the most satisfactory characters for limiting the group (see also Tate Regan 1923, Gosline 1965). Under the influence of Nybelin's interpretation of the uroneurals as dermal structures (urodermals), I proposed a provisional definition of the Teleostei based on two features of caudal structure, single centrum support of the two lower hypurals, and modification of the primary squamation of the caudal axis into elongate urodermals, in contact with the vertebral column and overlain by scales. It is necessary to reconsider these criteria, since although the first remains valid the second is meaningless: it is clear that the ural neural arches of pholidophorids, which were in contact with the notochord (normally uncalcified behind the first ural centrum) and are covered by scales, are homologous with and directly comparable with the uroneurals of *Leptolepis* and teleosts. But the caudal structures of pholidophorids described in this paper have strengthened my opinion that the caudal skeleton provides the best and most practicable means of limiting the Teleostei, and that the most logical level at which to place this limit is between the pholidophorids and the leptolepids.

There are trenchant anatomical differences between the caudal skeletons of pholidophorids and leptolepids (cf. Text-figs 1–6 with Text-figs 9, 10), but the tail in leptolepids is essentially similar to those of later teleosts. These anatomical differences between pholidophorids and leptolepids appear to have important functional significance. The essential change in the tail in the pholidophorid/leptolepid transition is the elimination of the oblique line of flexion, the " chondrostean hinge ", at the base of the axial lobe of the tail, by forward extension of the uroneurals across the level of the hinge to gain support from the perichordally ossified ural and pre-ural centra. On this basis, a definition of the Teleostei can be framed as follows: " Actinopterygian fishes in which the vertebral centra are perichordally ossified, the lower lobe of the caudal fin is primitively supported by two hypurals articulating with a single centrum, and in which the ural neural arches are modified into elongate uroneurals, the anterior uroneurals extending forwards on to the pre-ural centra ".

It is worth noting that on this definition there is no evidence from the structure of the tail that the living teleosts are polyphyletic. The uroneurals of the Elopomorpha, Clupeomorpha, Protacanthopterygii and Ostariophysi appear to be based on the pattern found in *Leptolepis dubia*, those of the Osteoglossomorpha (*Hiodon* and ichthyodectids) on the pattern found in *Allothrissops*, and both these patterns can be derived from the ural neural arches of *Leptolepis coryphaenoides* and pholidophorids. Other primitive teleostean caudal characters such as nineteen principal caudal rays, two ural centra, seven hypurals, three epurals, etc., occur in basal members of all the major teleostean groups.

(e) *Taxonomy and interrelationships of Lower Liassic Pholidophoridae*

Nybelin (1966) has written preliminary diagnoses of the family Pholidophoridae *s. str.* and the genera *Pholidophorus*, *Pholidolepis* and *Pholidophoropsis*. Information on the vertebral column and caudal anatomy of these fishes allows these diagnoses to be amplified as follows:

Family ***PHOLIDOPHORIDAE*** *sensu* Nybelin (1966)

Diagnosis: See Nybelin (1966 : 425) and add " vertebral centra consisting of calcifications in the sheath of the notochord, no perichordal centra, notochordal calcifications primarily in the form of opposed dorsal and ventral hemicentra; vertebrae diplospondylous in the middle part of the caudal region; eleven or twelve hypurals, only two lower hypurals; free ventral caudal radials at the tips of the last few haemal spines and the first hypural; seven or eight pairs of ural neural arches, those behind the first or second modified into elongated splints resembling the uroneurals of teleosts; four or five epurals; the seven or eight upper principal caudal rays elongated proximally, crossing the upper hypurals."

Genus ***PHOLIDOPHORUS*** Agassiz

Diagnosis. See Nybelin (1966 : 356) and add " notochord uncalcified behind the first ural centrum, first and second ural neural arches unmodified, four epurals, twenty-two to twenty-four principal caudal fin-rays, the uppermost hypaxial fin-ray reduced."

Genus ***PHOLIDOLEPIS*** Nybelin

Diagnosis. See Nybelin (1966 : 387) and add " notochord uncalcified beyond the second ural centrum, second ural neural arch modified, four epurals, twenty to twenty-one principal caudal rays, the uppermost hypaxial fin-ray reduced, four thick, rhombic scales (urodermals) at apex of squamation of upper caudal lobe, caudal scutes small, urodermals and caudal scutes without enamel, fulcra sometimes present on lower margin of tail."

Genus ***PHOLIDOPHOROPSIS*** Nybelin

Diagnosis. See Nybelin (1966 : 411) and add "notochord calcified in the ural region, second ural neural arch unmodified, five epurals, twenty-five to twenty-seven principal caudal fin-rays, uppermost hypaxial fin-ray unreduced, eight to ten thick, rhombic scales (urodermals) at apex of squamation of upper caudal lobe, caudal scutes large, urodermals and caudal scutes enamelled."

Nybelin (1966 : 427) has also discussed the interrelationships of *Pholidophorus*, *Pholidolepis* and *Pholidophoropsis*. Mainly on the structure of the preopercular, he concluded that *Pholidolepis* is probably derived from *Pholidophorus*, from which it differs primarily in thinning of the scales and loss of enamel, and that it possibly leads on to the leptolepids. *Pholidophoropsis* he found to belong in a different pholidophorid lineage, distinct from the *Pholidophorus*/*Pholidolepis* line at least since the Upper Trias. Thinning of the scales and reduction in enamel in *Pholidophoropsis* took place independently, and this genus shows little sign of relationship to the leptolepids. Nybelin's conclusions are fully borne out by the structure of the caudal skeleton in these fishes. Of the three genera, *Pholidolepis* is closest to the leptolepids and teleosts in the number of caudal fin-rays, the number of urodermals, absence of enamel on the fin-rays, urodermals and caudal scutes, fusion of the dorsal and ventral notochordal calcifications into complete rings, modification of the second ural neural arch and tendency to lose the fringing fulcra on the lower margin of the tail. Nothing in the structure of the tail of *Pholidolepis* indicates that it was not derived from *Pholidophorus*, and the presence of four epurals and a reduced uppermost hypaxial fin-ray in the two genera suggests that they are related. *Pholidophoropsis*, although it resembles *Pholidolepis* and teleosts in the cycloid scales and the presence of urodermals, differs from *Pholidolepis* and *Pholidophorus* in the series of notochordal calcifications in the ural region and could not have evolved from *Pholidophorus* because it is more primitive in having five epurals and a higher number of principal caudal rays.

IV. SUMMARY AND CONCLUSIONS

New anatomical facts and conclusions drawn from them in this paper include the following.

1. In the Lower Liassic Pholidophoridae *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis* the notochord was unconstricted and centra were formed only by opposed dorsal and ventral half-ring calcifications in the sheath of the notochord. There were no perichordal centra as there are in teleosts, and in the ural region the notochord was uncalcified except in *Pholidophoropsis*. The centra were diplospondylous in the middle part of the caudal region.

2. There are eleven or twelve hypurals in these fishes, three or four more than are known to occur in teleosts, but as in teleosts there were only two lower hypurals.

3. Ventral caudal radials are present in these pholidophorids at the tips of the last three haemal spines and the first hypural. Similar elements have not been found in teleost embryos and teleosts have probably lost the ventral caudal radials, not incorporated them in the haemal spines and hypurals.

4. There are four epurals in *Pholidophorus bechei* and *Pholidolepis*, five in *Pholidophoropsis*. In teleosts there are no more than three epurals while in primitive actinopterygians there are many. The epurals are detached neural spines, serial homologues of the supraneurals above the anterior vertebrae.

5. The uroneurals of teleosts are endoskeletal structures, derived from the seven or eight pairs of ural neural arches in pholidophorids, all but the first or second of which are modified into elongate, interlocking splints resembling teleostean uroneurals. In pholidophorids and primitive teleosts the first ural neural arch normally resembles the pre-ural neural arches, but in some individuals of *Leptolepis coryphaenoides*, *Hiodon* and possibly in ichthyodectids it is modified into a uroneural. In Upper

Jurassic *Thrissops* and *Allothrissops* and in primitive Osteoglossomorpha (*Hiodon* and ichthyodectids) all the uroneurals are elongate. In the Upper Jurassic *Leptolepis dubia* and in Elopomorpha, Clupeomorpha, Protacanthopterygii and Ostariophysi the uroneurals are differentiated into an anterior set of four long bones (ural neural arches 2–5) and a posterior set of three small bones (ural neural arches 6–8). In post-Jurassic teleosts fusion and loss reduce the number of separate uroneurals. *Alepocephalus* retains the most complete set of uroneurals among living teleosts.

6. Although the Lower Liassic pholidophorids could probably achieve neutral buoyancy, their tails were still functionally heterocercal, with an axial lobe stiffened by the upper hypaxial fin-rays and the ural neural arches which swung about an oblique line of flexion at which the modified ural neural arches, the upper hypaxial fin-rays, the pre-ural neural arches and the epurals ended. This line of flexion corresponds to the " hinge " in palaeoniscoid tails at which the scale-rows change their orientation. In teleosts this " hinge " is obliterated, primarily by forward extension of the uroneurals. Teleostean uroneurals serve to equalize the flexibility of the upper and lower lobes of the tail so that it functions homocercally, and first the fin-rays and later the endoskeleton achieve dorso-ventral symmetry.

7. Precocious replacement of perichondral and endochondral bone by membrane bone accounts for the mode of ossification and " dermal " appearance of the uroneurals in teleosts.

8. In *Pholidophorus bechei* the caudal skeleton is covered by thick, rhombic enamelled scales. In *Pholidolepis* and *Pholidophoropsis* the trunk scales have lost their enamel and become thin and cycloid, but a patch of thick, rhombic scales persists at the apex of the reduced body lobe of the tail. One or two of these scales persist on the upper hypaxial fin-rays in a few primitive teleosts as urodermals. In Jurassic teleosts (*Leptolepis*, *Allothrissops*) there are one or two urodermals, in post-Jurassic teleosts no more than one is known. *Elops*, *Coregonus*, *Osmerus*, and *Argentina* are the only living teleosts known to retain a urodermal.

9. A definition of the Teleostei is proposed based on the single centrum support of the lower hypurals and the forward extension of the uroneurals on to the pre-ural centra. This definition includes the leptolepids in the Teleostei.

10. Nybelin's account of the interrelationships of the Lower Liassic pholidophorids is confirmed by caudal structure. Of the three genera dealt with here, *Pholidolepis* is closest to the teleosts.

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WEITZMAN, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford ichthyol. Bull.*, Palo Alto, **8** : 1–77, 21 figs.

WHITEHOUSE, R. H. 1910. The Caudal Fin of the Teleostomi. *Proc. zool. Soc. Lond.*, **1910** : 590–627, pls. 47–50.

ADDENDUM

While this paper was in press R. Lund (1967, An analysis of the propulsive mechanisms of fishes, with reference to some fossil actinopterygians. *Ann. Carneg. Mus.*, Pittsburgh, **39**: 195–218, 12 figs.) published a discussion of the actinopterygian tail, including photographs of excellent caudal skeletons of several Jurassic genera. On questions dealt with in the present paper, the structure and nomenclature of the teleostean caudal skeleton, Lund reaches radically different conclusions from my own. Some of Lund's arguments, such as his identification of the uroneurals as intermuscular bones, are answered above, and the only points which will be mentioned here concern the nomenclature of the teleost tail. Lund rejects Nybelin's characterisation of the boundary between the ural and pre-ural regions as the point at which the caudal vessels bifurcate, writing "this point varies greatly in the teleosts" and is "modified by function". He defines hypurals as all haemal spines supporting caudal fin-rays and ural centra as all centra supporting such spines—"haemal spines that support fin-rays are *ipso facto* specialized . . . it is necessary to give these specialized haemal spines a collective name". Lund gives no evidence of variation in the point of bifurcation of the caudal vessels: my own experience and that of workers who have examined large series of teleost caudal skeletons (Goslind 1965: 191; Monod 1967: 113) is that this point is constant. And Nybelin's terminology does provide a collective name, "pre-ural haemal spines", for haemal spines supporting caudal fin-rays. The number of pre-ural haemal spines supporting fin-rays must be specified in each case simply because it varies intraspecifically (e.g. Hollister 1937, figs. 4–6; Weitzman 1962: 39).

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PLATE 1

Pholidophorus bechei Agassiz. Posterior part of vertebral column and base of caudal fin of 19010 (see also Text-fig. 1). ×5·5.

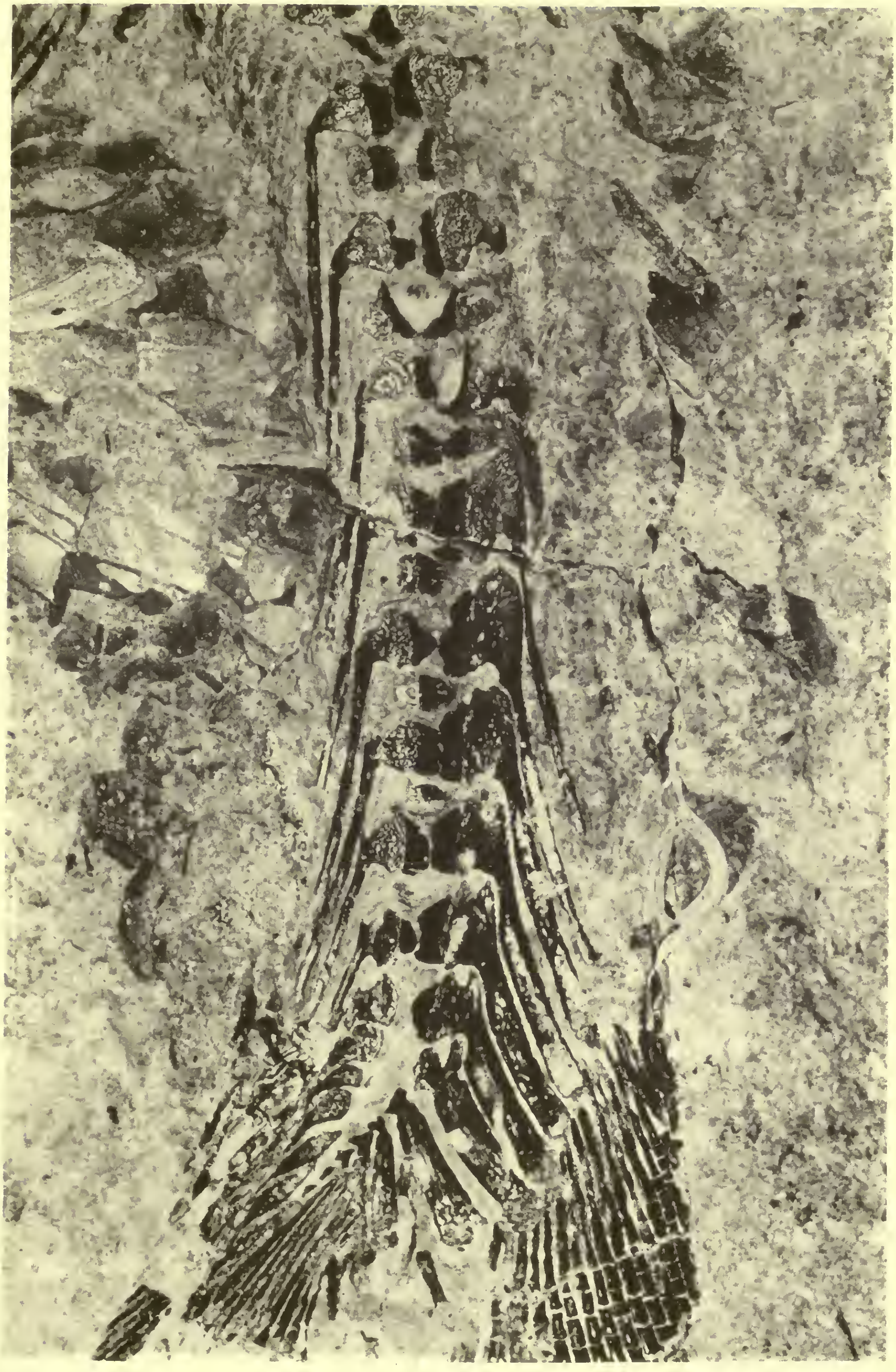


PLATE 2

Pholidolepis dorsetensis Nybelin. Posterior part of vertebral column and base of caudal fin of P.6067 (see also Text-fig. 3). ×7.

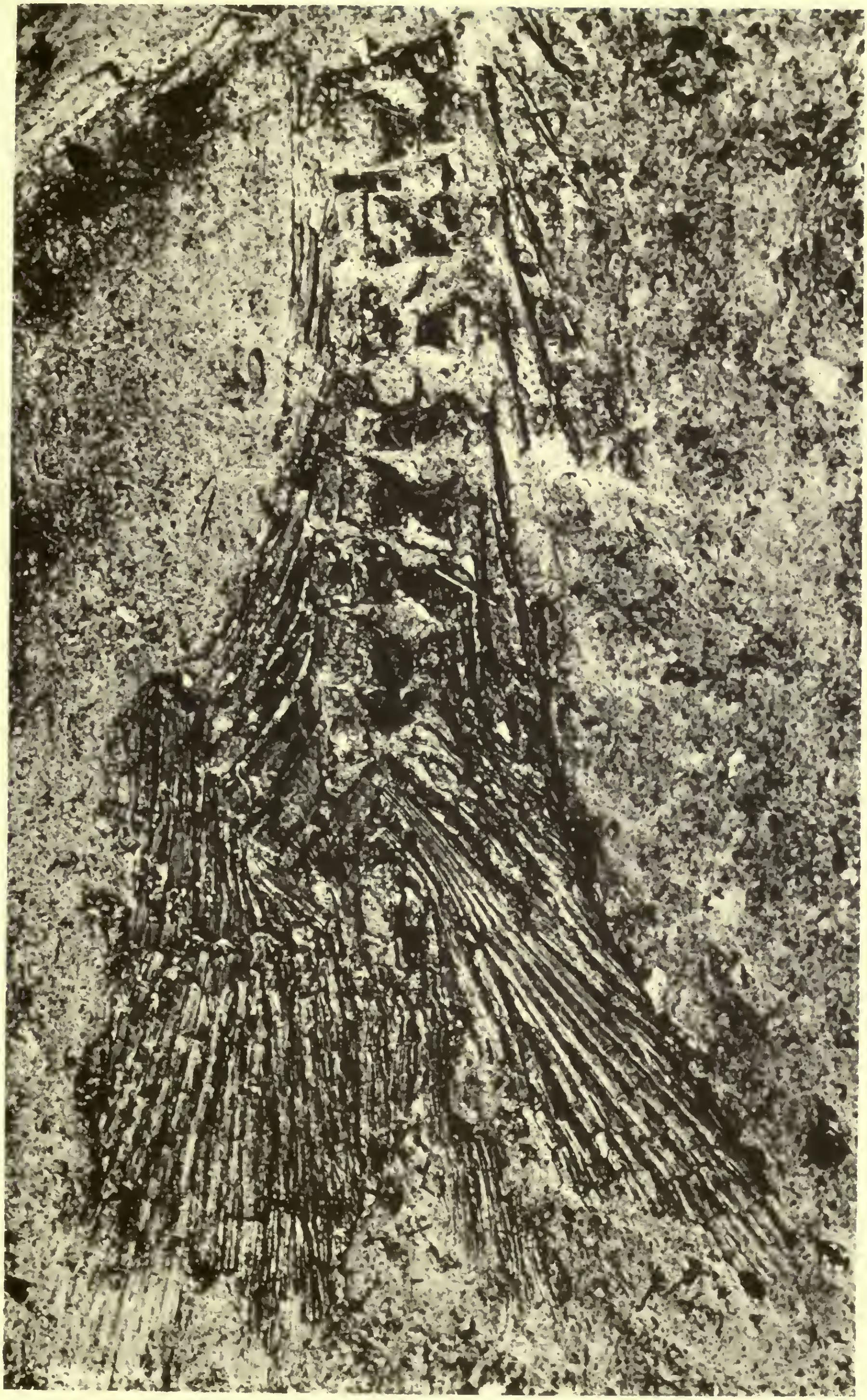
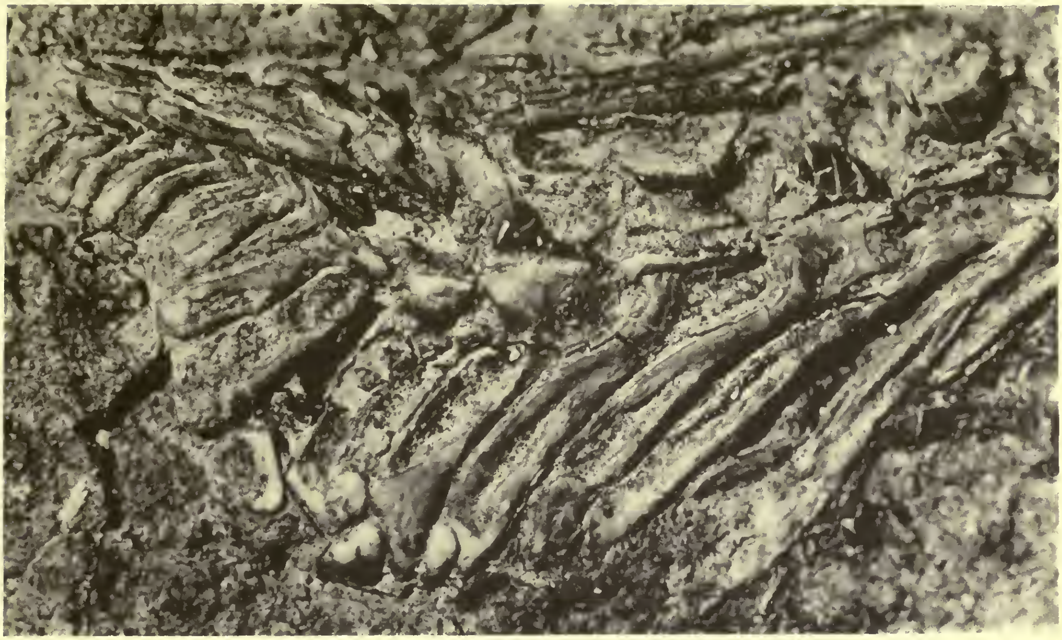


PLATE 3

Fig. 1. ***Pholidophorus bechei*** Agassiz. Caudal skeleton of RSM 1888.61.73 (see also Text-fig. 2A). ×7.

Fig. 2. ***Pholidolepis dorsetensis*** Nybelin. Caudal skeleton of P.44709 (see also Text-fig. 4A). ×10.



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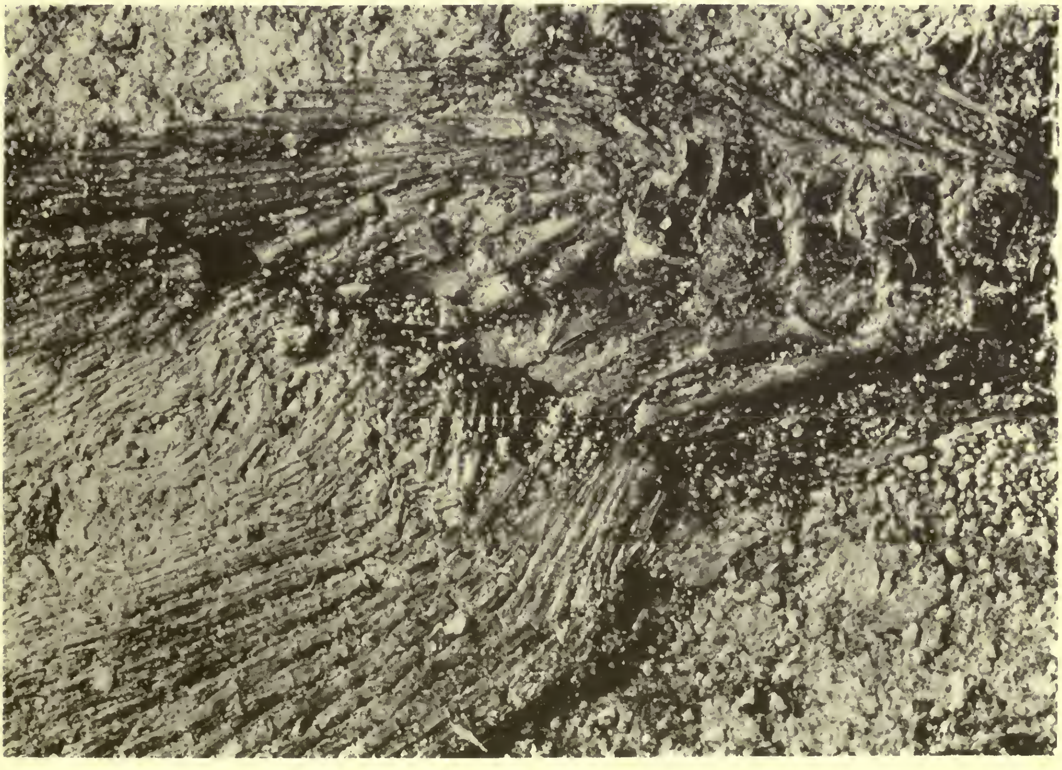

2

PLATE 4

Pholidophoropsis maculata Nybelin. Posterior part of vertebral column and caudal skeleton of P.7582 (see also Text-fig. 6). ×5·5.

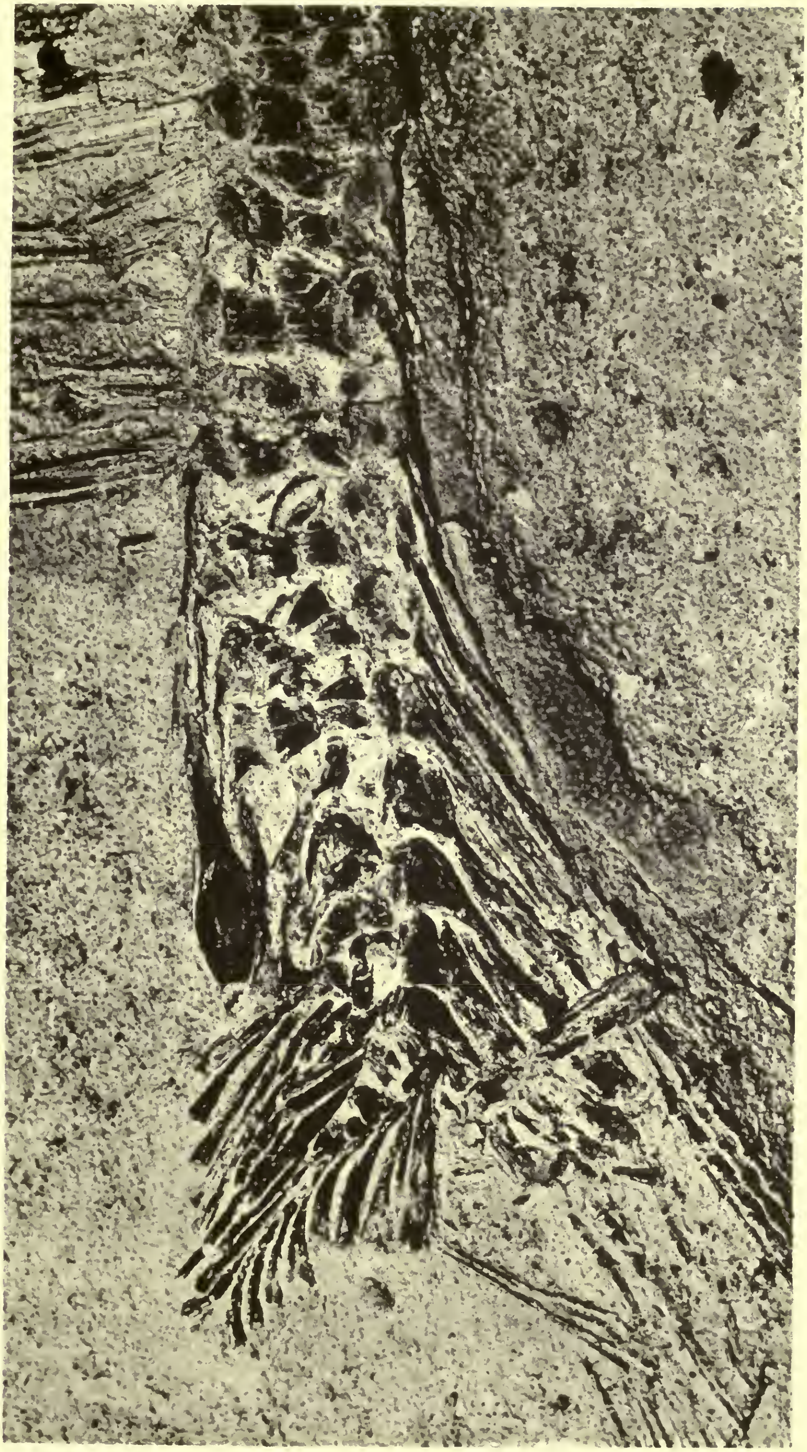

PLATE 5

FIG. 1. ***Pholidophorus bechei*** Agassiz. Base of upper caudal lobe of P.154, showing the epurals (*ep 1–4*), the second to fifth ural neural arches and the heads of the upper hypurals. ×25.

FIG. 2. ***Pholidolepis dorsetensis*** Nybelin. Base of the upper hypaxial fin-rays of P.44707, showing three urodermals (*ud*); the fourth urodermal is only preserved in impression in this specimen. ×25.

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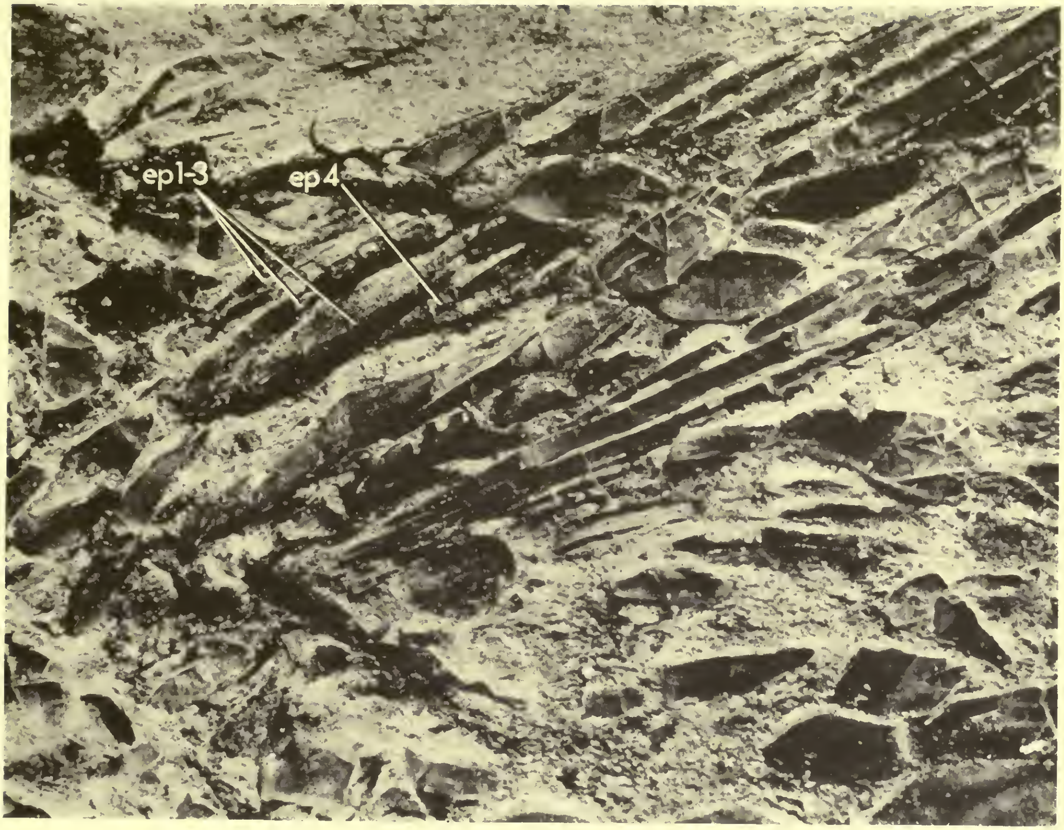

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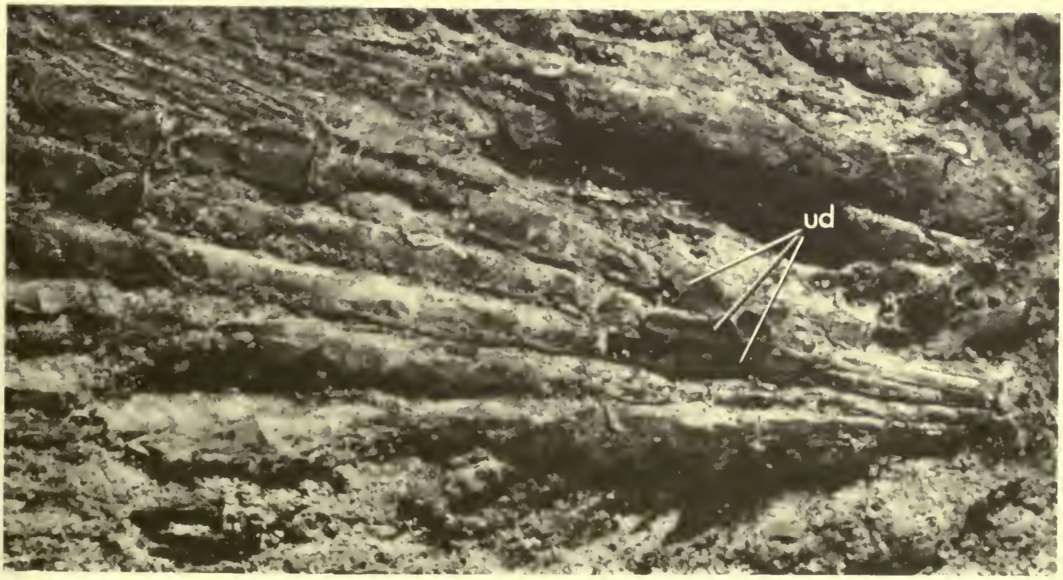

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THE SUBPHYLUM CALCICHORDATA (JEFFERIES 1967) PRIMITIVE FOSSIL CHORDATES WITH ECHINODERM AFFINITIES

R. P. S. JEFFERIES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 6
LONDON: 1968

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- 5 JUL 19
NATURAL HISTO

THE SUBPHYLUM CALCICHORDATA (JEFFERIES 1967) PRIMITIVE FOSSIL CHORDATES WITH ECHINODERM AFFINITIES

BY

RICHARD PETER SPENCER JEFFERIES x-ref.

Pp. 241–339*; 10 plates; 27 text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 6
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 16, *No.* 6 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

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THE SUBPHYLUM CALCICHORDATA (JEFFERIES 1967) PRIMITIVE FOSSIL CHORDATES WITH ECHINODERM AFFINITIES

By RICHARD PETER SPENCER JEFFERIES

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SYNOPSIS

The orders Cornuta (Jaekel 1900) and Mitrata (Jaekel 1918), which constitute the class Stylophora (Gill & Caster, 1960) (Cambrian to Devonian) and which are customarily placed in the Echinodermata, are transferred to the Chordata as the Subphylum Calcichordata (Jefferies 1967). With Gislén (1930), the Calcichordata are regarded as ancestral to the Urochordata, Cephalochordata and Craniata.

The cornutes *Cothurnocystis elizae* Bather and *C. curvata* Bather had external branchial slits in the left, dorsal part of the theca that were mechanically adapted as outlet valves. The mouth was near the anterior end of the theca. The anus, situated left of the stem, was external in *C. elizae* but opened into the most median gill slits in *C. curvata*. Anterior and posterior coeloms, pharynx and buccal cavity can be recognized in the theca. The stem, which is homologous with both the stem of a crinoid and the tail of a fish, had an anterior part for lateral flexion, a posterior part adapted for upwards flexion and a medial rigid part containing a ventral massive element, the stylocone. In the posterior stem evidence indicates the presence of segmental muscle blocks, a median chambered organ or notochord and probable paired segmental blood vessels. The brain or aboral nerve centre was at the anterior end of the stem.

The mitrates *Mitrocystella incipiens* (Barrande) *miloni* Chauvel and *Mitrocystites mitra* Barrande had paired, posterior gill openings and presumed, paired, internal gill slits. The mouth was at the anterior end of the body and pointed somewhat leftwards, particularly in juvenile *M. mitra*, like the mouth of larval amphioxus. Anterior and posterior coeloms, left and right pharyngeal chambers, buccal cavity and paired posterior atria can be recognized in the theca. The rectum opened into the left atrium as in a living tunicate tadpole. Left gill slits probably preceded right gill slits in ontogeny as in amphioxus. The stem, as in cornutes, had anterior, medial and posterior parts. The anterior part was probably adapted to lateral flexion, the medial part contained a massive dorsal element (styloid), and the posterior part was adapted for flexing downwards. In the posterior stem, evidence indicates the presence of segmental muscle blocks, notochord, dorsal nerve cord, paired segmental ganglia and a complicated vascular system. The brain was at the anterior end of the stem and was fish-like in character with optic, hypophyseal, medullary and olfactory parts. The cranial nerves were complicated and included homologues of the trigeminal complex and trigemino-profundus ganglia and of the olfactory, optic and lateralis complexes of fish.

The extant chordate subphyla probably derived from a primitive, probably Upper Cambrian, mitrate that became free swimming.

The following homologies are suggested between chordates and crinoids: notochord = chambered organ; dorsal nerve cord = peduncular nerve; longitudinal vessel broadly = haemal strand; brain = aboral nerve centre; cranial nerves broadly = aboral nerves to theca.

Ubaghs' interpretation of the stem of Stylophora (1961*b*) is rejected as also is the classical theory of vertebrate head segmentation. Lindström's (1949) interpretation of the cranial nerves of cephalaspids is adopted as the most reasonable yet proposed.

I. INTRODUCTION

THE subjects of this paper are certain bizarre fossils, conventionally regarded as echinoderms, belonging to the orders Cornuta Jaekel 1900 and Mitrata Jaekel 1918. The conclusion is reached, with Gislén (1930), that, while having definite echinoderm affinities, they are better placed in the Chordata, and are the ancestors of other Chordata, including tunicates, Amphioxus and the vertebrates.

The Cornuta and Mitrata are conventionally regarded as members of Jaekel's Class Carpoidea 1900. This is usually defined as including the orders Cornuta, Mitrata, Soluta, Cincta and Digitata (e.g. Gill & Caster 1960 : 11). The extent to which the Carpoidea are a natural group is doubtful. It is certain, however, as shown below, that Cornuta and Mitrata are closely allied to each other. They were placed by Gill & Caster (1960 : 11) in the distinct Superorder Stylophora, here regarded as a class.

A relationship between echinoderms, hemichordates and chordates is widely accepted (p. 327). The suggestion that Cornuta and Mitrata are in fact chordates, and ancestral to other chordates, is therefore inherently plausible. It was mentioned in passing by Matsumoto (1929 : 27) and argued in detail, and with great erudition, by Gislén (1930). Gislén's views were mentioned favourably by Gregory (1935 : 280; 1936 : 321; 1946 : 358), Caster (1952 : 37), and Caster & Eaton (1956). They have not been widely accepted, however, mainly because Gislén's argument was based on embryology rather than fossils, and his reconstruction of the soft parts of cornutes and mitrates was little more than guesswork. Berrill (1955 : 5) dismissed Gislén's hypothesis in a paragraph. Marcus (1958 : 50), however, expressed the view that " Future evidence of the origin of the Chordata from the Carpoidea would by no means be surprising."

I agree with Gislén's broad results and with some of his major anatomical suggestions such as the position of the mouth in cornutes and mitrates and of gill slits in cornutes, the homology of carpoid stem and fish's tail, and the homology of some of the asymmetries of larval *Amphioxus* with those of mitrates and cornutes. Most of Gislén's detailed arguments, however, seem to be incorrect.

Other works dealing with the morphology of mitrates and cornutes generally agree on details but flatly disagree on essentials. Among the most important are Jaekel (1900; 1918), Bather (1913; 1928), Chauvel (1941) and Ubaghs (1961*a*; 1961*b*; 1963). Chauvel's reconstruction of the nervous system of *Mitrocystella* is a *tour de force* and Ubaghs' observations on the details of stem structure are also highly important, though his conclusions are not acceptable.

The present work takes the form of a detailed morphological study of the cornutes *Cothurnocystis elizae* Bather and *C. curvata* Bather, and the mitrates *Mitrocystella incipiens* (Barrande) *miloni* Chauvel and *Mitrocystites mitra* Barrande. These forms were chosen because they are reasonably large (theca about 3 cm. across), well represented in the British Museum (Natural History) collections and preserved largely as hollow moulds, with the skeletal calcite dissolved away. This allows the internal mould to be examined direct and the form of the skeleton to be obtained by means of latex and dental rubber casts. The reconstructions, based on observations of as many specimens as possible, were drawn in several projections simultaneously on a drawing board. Supplementary observations were made on *Ceratocystis perneri* Jaekel, *Phyllocystis blayaci* Thoral, *P. crassimarginata* Thoral, *Chinianocarpos thorali* Ubaghs, *Lagynocystis pyramidalis* (Barrande) and *Peltocystis cornuta* Thoral.

In reconstructing the soft parts, a functional explanation has been sought for as many features as possible. It was assumed that the soft parts of the four species mainly studied were fundamentally the same. The fossils have been interpreted by analogy first with crinoids, and secondly with tunicate larvae and fish.

The results flatly contradict the idea of a completely segmented vertebrate ancestor with mandibular and premandibular gill slits which is so firmly embedded in classical vertebrate anatomy (e.g. Goodrich 1918) but for which the evidence is, in fact, very weak (Kingsbury 1926). They agree somewhat better with the views of students of tunicates such as Berrill (1955) and Garstang (1928), except that there is no evidence of neoteny. They also agree better with the account of cephalaspid cranial anatomy given by Lindström (1949) than with that of Allis (1931), Wangsjö (1952) or Stensiö (1927; 1958). Wangsjö's interpretations are preferable in many respects to Stensiö's but Lindström's seem more reasonable than either.

As regards nomenclature, the terms anterior, posterior, dorsal and ventral, right and left are used as for a fish. The plate nomenclature is a much modified version of that of Jaekel (1900). The nomenclature of Caster (1952) could not be used, since a scheme was needed that was applicable to both cornutes and mitrates and which was not too dependent on the correct homology of plates. The following notation is employed: C = a central dorsal plate of the theca, D = a dorsal plate of the anterior stem, M = a marginal plate, S = a ventral spike, V = ventral plate of theca, VS = ventral plate of stem, suffix $_{\mathrm{A}}$ = anterior, suffix $_{\mathrm{D}}$ = dorsal, suffix $_{\mathrm{L}}$ = left, suffix $_{\mathrm{R}}$ = right, suffix $_{\mathrm{V}}$ = ventral, suffix $_{(0)\ 1,\ 2,\ 3}$ etc. indicates position in sequence counting from anterior end of stem.

A brief account of the work described in the present paper has already been published (Jefferies 1967), and in that work the name Calcichordata was used for the first time. Since writing that brief account I have changed my mind on some details. Thus the median line nerves of cornutes cannot represent the optic nerves (n_3) of mitrates since they pass ventral to the gut. They may possibly correspond to the nerves n_0 of mitrates. Again, the peripheral canals of *M. incipiens miloni* probably did not extend forwards to open in the olfactory openings. Consequently the fibres of the olfactory nerves did not travel anteriorly in the peripheral canals, and did not have to leave these to reach the telencephalon. The reconstruction of the anterior parts of the nerves n_2 of *M. mitra* has been altered in some respects. Further it no longer seems likely, though it is still possible, that the Cephalochordata derived from a different group of mitrates to the Urochordata and Craniata. The probable position of the oesophagus of *M. i. miloni* and the probable ontogenetic origin of the posterior coelom of *M. i. miloni* and *M. mitra* were not discussed in the earlier paper. None of these are very important points and they do not affect the fundamental thesis here advanced.

II. ACKNOWLEDGMENTS

The author gratefully acknowledges the help of numerous colleagues. Dr. W. T. Dean initiated the investigation by finding a mitrate from Shropshire that he discussed with the author. Mr. H. G. Owen and Mr. A. E. Rixon have been very helpful in technical matters. Drs. Horný and Zazvorká of Prague, M. Mattei of Montpellier, Prof. Milon of Rennes, Dr. B. Kummel of Harvard and Prof. David of Lyon, have allowed specimens in their charge to be examined. Prof. J. E. Smith made available the facilities of the Marine Biological Station, Plymouth and Dr. D. B. Carlisle introduced me there to living tunicates. Innumerable colleagues have discussed the subject with the author, helping to clarify ideas, and making many suggestions. In this respect I would particularly like to mention Dr. E. I. White, M. J. Chauvel, Dr. R. Prokop, Dr. Q. Bone, Dr. G. Underwood, Dr. D. B. Macurda, Prof. J. Wyatt Durham, Dr. N. J. Holmes, Dr. M. H. Hey, Dr. C. Patterson and Dr. C. R. C. Paul. Prof. Ubaghs gave the author the chance to see much unpublished work. Our agreement on facts was combined with almost complete disagreement on interpretation. Mr. P. Minton generously gave several afternoons to discussion and made numerous helpful suggestions on functional morphology from an engineer's standpoint. Text-figures 1a, b; 2; 4b, d; 6; 8a, b; 11a; 13a, b, 14a, b; 17b; 19a; 20; 21; 23a, b; and 27a are reproduced here by kind permission of the Zoological Society of London.

III. MORPHOLOGY

a. ***Cothurnocystis elizae*** Bather 1913

Systematic position: Phylum Chordata: Subphylum Calcichordata: Class Stylophora (Gill & Caster 1960). Order Cornuta (Jaekel 1900). Family: Cothurnocystidae Bather 1913. Genus: *Cothurnocystis* (Bather 1913). Type species.

Occurrence: Only known from the hard, greenish siltstone of the Starfish Bed [Upper Ordovician, Ashgill Series, Drummuck Group]. All the material examined was from Thraive Glen, Girvan, Ayrshire, Scotland—the type locality. The associated fauna indicates a shallow water, marine environment.

Material: About 190 specimens collected by the Gray family and preserved in the British Museum (Natural History). The specimens are mostly still articulated as if suddenly buried. The plates have not been distorted by compaction of the rock. The registration numbers are as follows: E 23130–1, E 23133–7, E 23139–41, E 23143–50, E 23152–9, E 23161–4, E 23166–7, E 23169–72, E 23174–86, E 23188–93, E 23201, E 23318, E 23329, E 23337, E 23342, E 23352, E 23394–6, E 23702–5, E 23713, E 23716–7, E 23719–27, E 23729, E 23731–7, E 23740–3, E 23745, E 23747, E 23749, E 23752–3, E 23757, E 23761, E 23766, E 28417, E 28420, E 28571–3, E 28575, E 28590–1, E 28603–8, E 28631–2, E 28635–46, E 28651, E 28654, E 28656–60, E 28663–4, E 28666–7, E 28884.

GENERAL SHAPE AND PLATE NOMENCLATURE: (Fig. 1a–g).

The animal consists of a theca and a stem. The theca is boot-shaped and, following Bather, an " ankle " and a " foot " part can be distinguished. The thecal skeleton consists of stout marginal plates to which are attached upper dorsal and lower ventral flexible integuments (" obverse " and " reverse " Bather 1913). The recognition of upper and lower surfaces of the theca is virtually certain, for all the thecal openings are on the dorsal side, and all the spikes for anchoring the theca to the bottom are ventral. Three prominent spines project from the anterior face of the theca and can be called the right oral appendage, left oral appendage and left appendage (tag, tongue and toespine of Bather 1913: 399; digital, glossal and spinal of Ubaghs 1963).

The marginal plates are numbered to right and left starting anterior to the stem and finishing at the mouth, the complete assemblage being as follows:

Notation	Name	Bather 1913	Ubaghs 1963. Based on plate notation of Jaekel 1900
M_{1LD}	first left dorsal marginal	Not shown	Not shown
M_{1LV}	first left ventral marginal	5	M_1
M_{2L}	second left marginal	6	M_2
M_{3L}	third left marginal	7	M_3
M_{4L}	fourth left marginal (incl. left appendage)	8 (incl. toe spine)	M_4 (incl. spinal)
M_{5L}	fifth left marginal	9 and 10	M_5 and M_6
loap	left oral appendage	tongue	glossal
M_{6L}	sixth left marginal	11	M_7
M_{1RD}	first right dorsal marginal	Not shown	Not shown
M_{1RV}	first right ventral marginal	4	M_1'
M_{2R}	second right marginal	3	M_2'
M_{3R}	third right marginal	2	M_3'
M_{4R}	fourth right marginal	1	M_4'
roap	right oral appendage	tag	digital
M_{5R}	fifth right marginal	12	M_5'

A strut on the ventral surface connects M_{1R} and M_{5L}. Distinct spikes (S) are present on the ventral surfaces of M_{2R} (S_R), M_{2L} (S_{1L}), and M_{3L} (S_{2L}). Sutures are indicated $M_{1LD/V}$, $M_{2/3R}$ etc.

The stem consists of three distinct parts: anterior, medial and posterior. The nomenclature used will be discussed later (p. 259ff).

THECAL OPENINGS: The openings of the theca are anatomically crucial and have caused much argument.

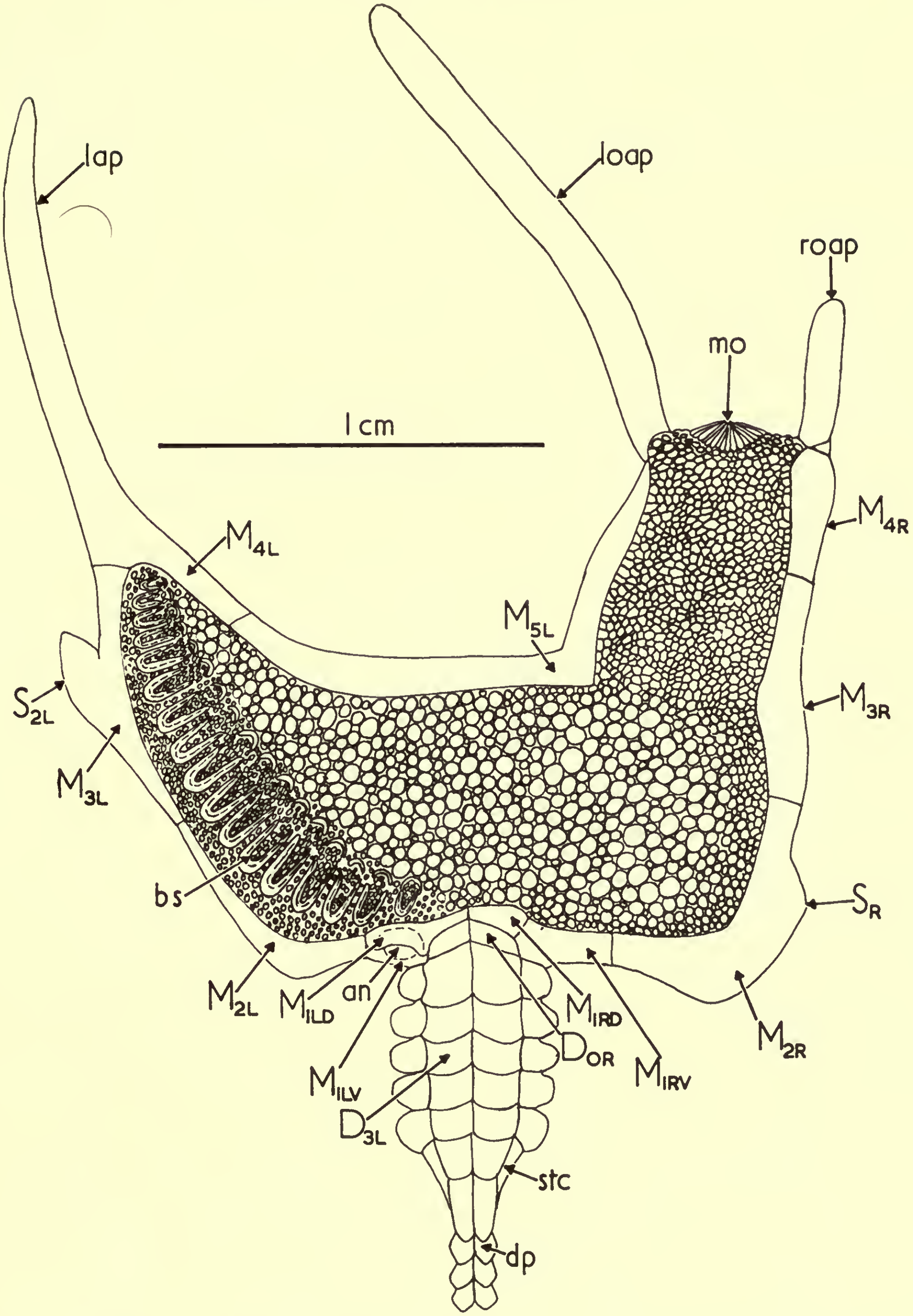

lap
loap
roap
mo
1 cm
M_{4L}
M_{4R}
M_{5L}
S_{2L}
M_{3R}
M_{3L}
bs
S_R
M_{2L}
M_{1LD}
an
M_{1RD}
D_{OR}
M_{1RV}
M_{2R}
M_{1LV}
D_{3L}
stc
dp

FIG. 1. *Cothurnocystis elizae.* Reconstruction of external features. a. dorsal ; b. ventral aspect ; c. stem from left ; d. theca from left ; e. "ankle" region from left ; f. theca from right ; g. posterior aspect. an = anus ; dp = dorsal plate of posterior stem ; lap = left appendage ; loap = left oral appendage ; roap = right oral appendage ; stc = stylocone ; str = strut ; vo = ventral ossicle without boss ; vob = ventral ossicle with boss.

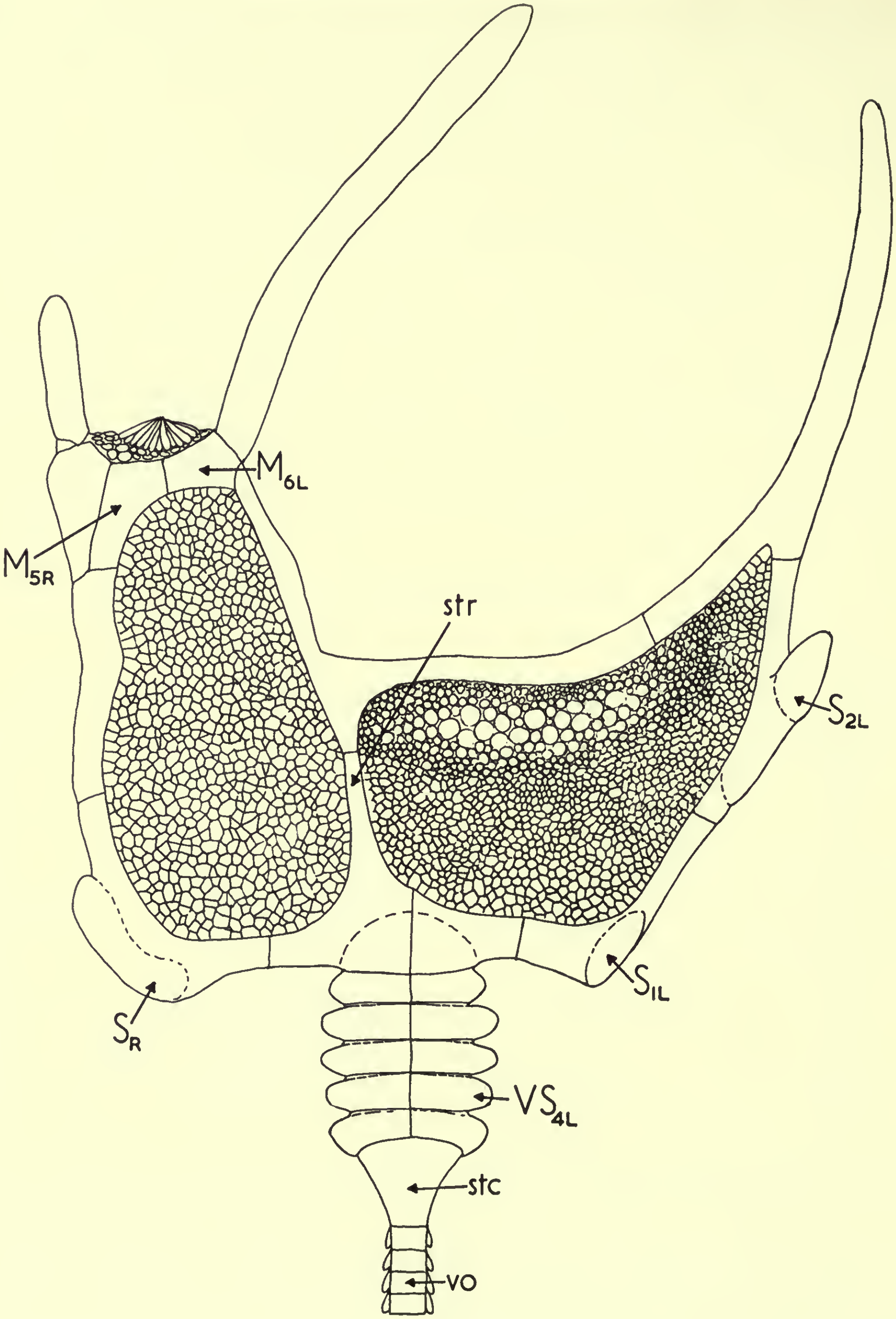

M_{6L}
M_{5R}
str
S_{2L}
S_{1L}
S_R
VS_{4L}
stc
vo

Fig. 1b.

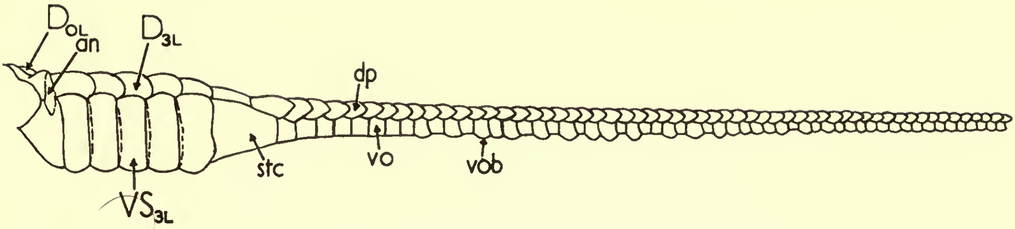

D0L
an
D3L
dp
stc
vo
vob
VS3L

FIG. 1c.

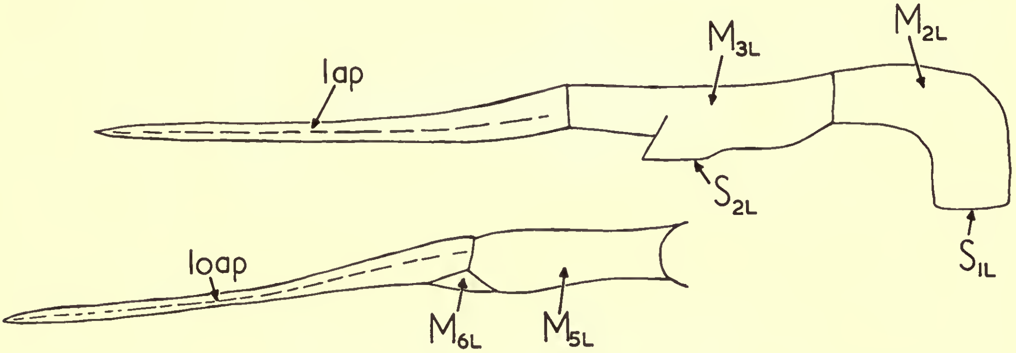

lap
M3L
M2L
S2L
S1L
loap
M6L
M5L

FIG. 1d, e.

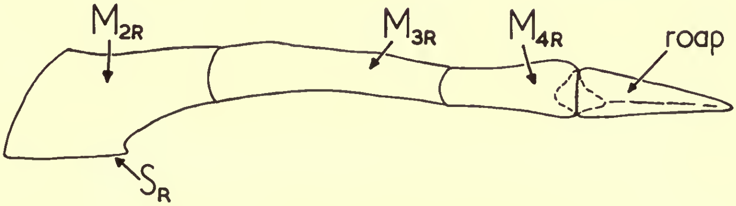

M2R
M3R
M4R
roap
SR

FIG. 1f.

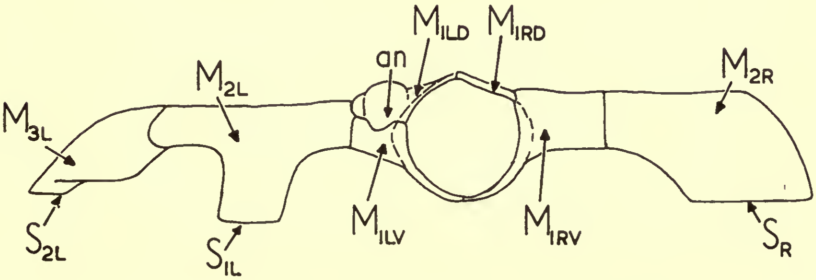

M1LD
M1RD
an
M2L
M2R
M3L
S2L
S1L
M1LV
M1RV
SR

FIG. 1g.

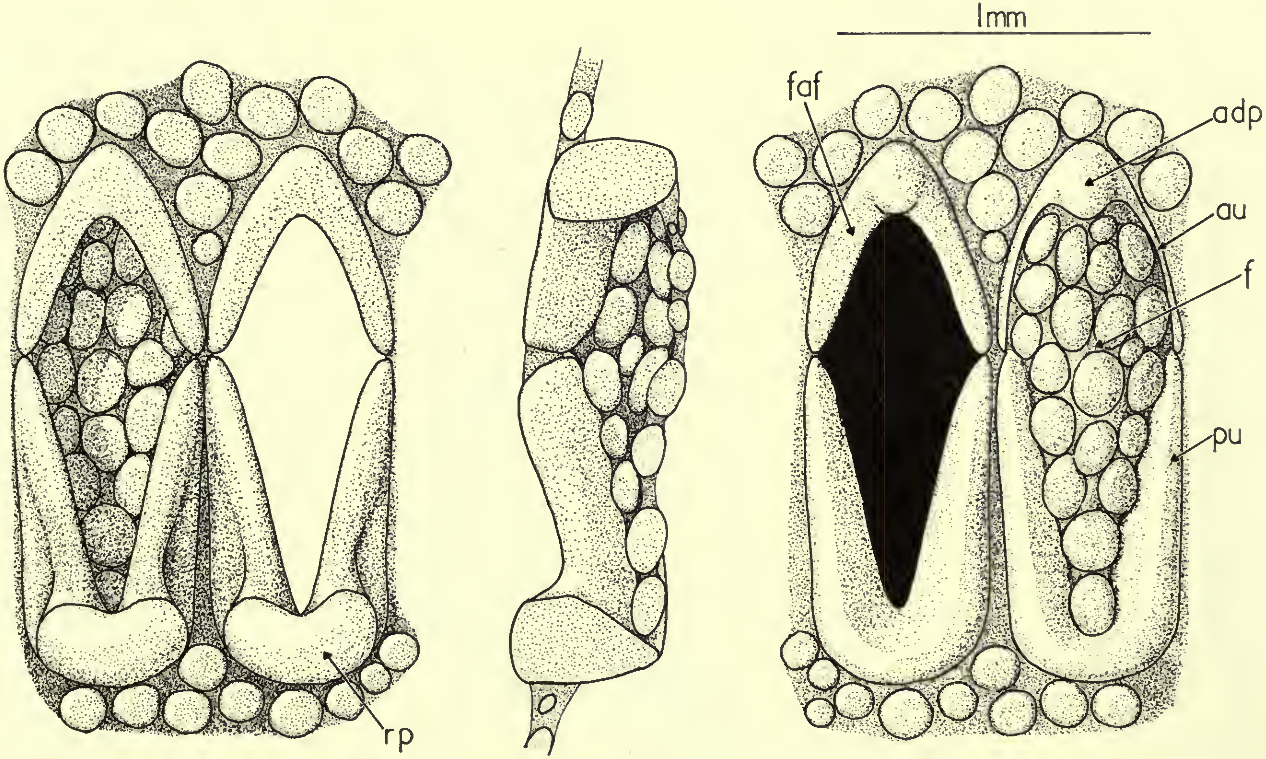


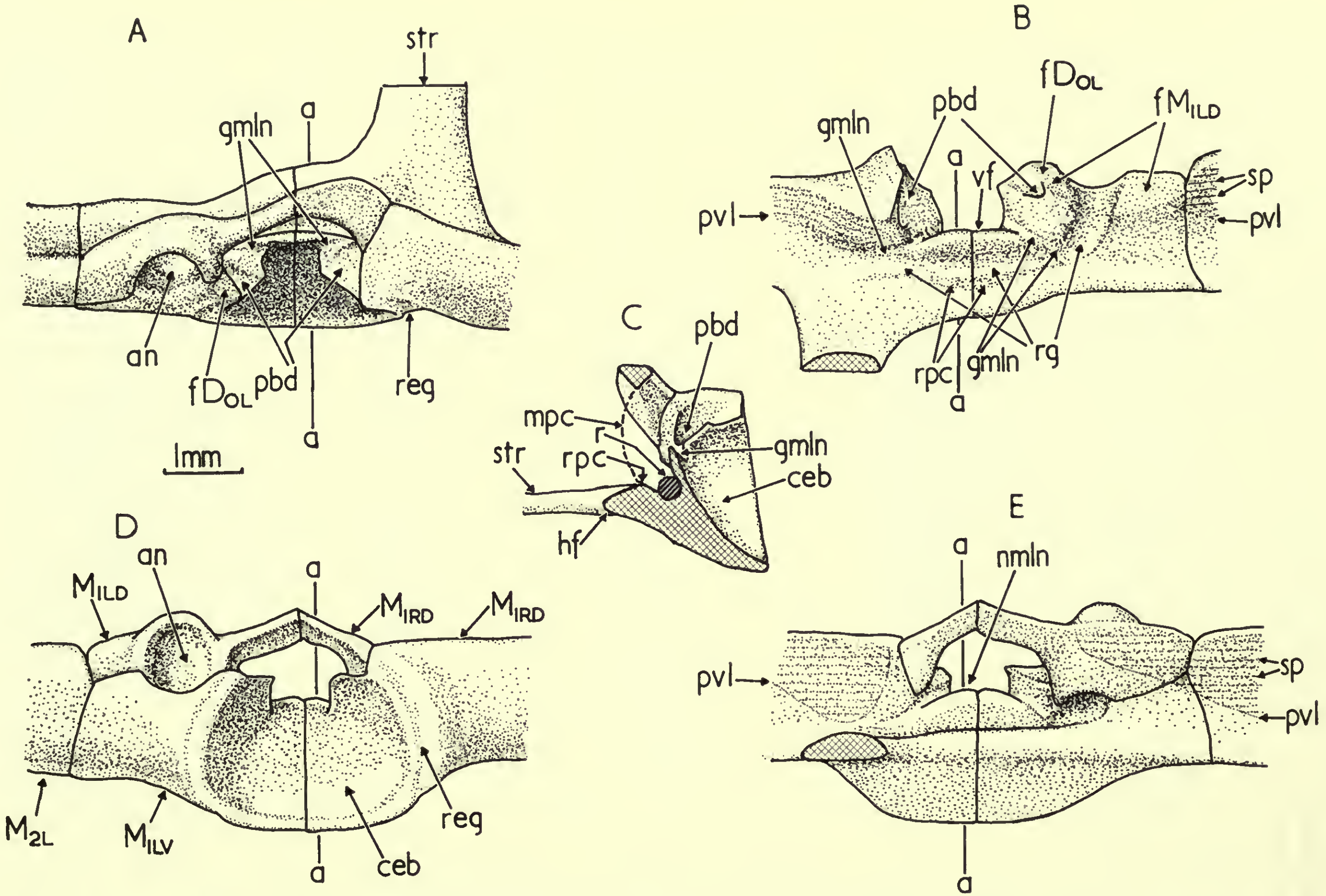
FIG. 2. *C. elizae.* Structure of branchial slits. a. internal aspect ; b. longitudinal section; c. external aspect. adp = antero-dorsal process ; au = anterior u-plate ; f = flap ; faf = flap attachment facet ; pu = posterior u-plate ; rp = reniform process.

There were, first, about 16 elliptical openings (bs) in the left, posterior part of the dorsal integument. Their detailed structure (Fig. 2 a–c; Pl. 1, figs. 1, 7, 8) can best be studied with latex casts. Each opening is surrounded by a frame consisting of a smaller anterior u-shaped plate (au) and a larger posterior one (pu) with an articulation between them. The anterior dorsal part of the anterior u-plate bears an antero-dorsal process (adp), of very variable size. Posterior to this process a flap (f) is attached by flap attachment facets (faf). This flap is convex outwards and concave inwards and contains many small plates which are often bigger towards the margins than in the middle of the flap. The flap must have been flexible in life and the edges of its free, posterior part were able to rest on the posterior u-plate, so as to shut the opening completely. There is no doubt that the flap was attached to the anterior u-plate rather than the posterior one since, when these two plates were displaced relative to each other after death, the flap was sometimes displaced to one side of the posterior u-plate (flaps f in Pl. 1, fig. 8) but remained connected to the anterior u-plate in the normal way. The posterior, internal end of the posterior u-plate was produced into a flat-topped reniform process (rp in Fig. 2a; Pl. 1, fig. 1).

Bather's descriptions of these openings (1913 : 404, fig. 16) is very different from the above except as regards the two u-plates of the frame. In his view the small plates inside each slit were biserial " cover plates " attached to the edges of the posterior u-plate. This interpretation may have been suggested by the fact that the plates round the edge of each flap tend to be larger than those in the middle. Using latex casts, however, which were not of course available to Bather, the attachment of the flap to the anterior rather than the posterior u-plate can easily be demonstrated.

The structure of these openings strongly suggests outlet valves. When the water pressure beneath the branchial slits increased, the flaps would lift from the posterior u-plates. This would happen partly because of the flexibility of the flaps, and partly because the frames of the slits would bend upwards at the articulations between anterior and posterior u-plates, to follow the bulging of the integument. When the flaps opened water would escape. As the water pressure beneath the openings consequently decreased, the flaps would close and prevent water from entering. The outwardly convex, arcuate section of each flap, maintained by the u-shape of the anterior u-plate and by a slight stiffness imparted by the little plates of the flap, is admirably suited to resist pressure from outside and confirms the outlet valve interpretation. This interpretation is also supported by the presence of a differently constructed outlet-valve system in a corresponding position in *C. curvata* (p. 266). The slits of both species do not resemble inlet structures and Bather's view that they were mouths, resting as it does on the interpretation of the flap plates as biserial cover plates, is without foundation. It is unlikely that the slits were gonadial (*pace* Jaekel 1918 : 122) or excretory since a much less elaborate structure would, in these cases, suffice. By far the most probable interpretation is that they were exhalent and homologous with branchial slits, as Gislén suggested (1930 : 213).

Another opening, not mentioned in the literature (an in Figs. 1a, g, Fig. 3a, d;


A
str
a
gmln
an
fDOL
pbd
a
reg
1mm
B
fDOL
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vf
sp
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mpc
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ceb
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an
MILD
a
MIRD
MIRD
M2L
MILV
a
ceb
reg
E
a
nmln
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sp
pvl
a

FIG. 3. *C. elizae.* Structure of region just anterior to stem. A. dorsal ; B. anterodorsal aspects ; C. longitudinal section through a–a ; D. posterior ; E. anterior aspects. an = anus ; ceb = cerebral basin ; fD_{OL} = facet for D_{OL} ; fM_{1LD} = facet for M_{1LD} ; gmln = groove for median line nerve ; hf = horizontal flange of M_{1R} and LV ; mpc = membrane limiting posterior coelom anteriorly ; nmln = notch for median line nerves ; pbd = depressions for pyriform bodies ; r = rectum ; reg = reception groove for auterior stem ; rg = rectal groove ; rpc = ridge limiting posterior coelom anteriorly ; sp = striations of pharynx ; vf = vertical flange of M_{1L} and RV ; str = strut.

Pl. 1, figs. 2, 10) whose function was clearly different from that of the gill slits, lies just posterior to the most median of these, to the left of the stem, on the suture M_{1LV}/M_{1LD}. It connects with a groove (rg) which first goes down vertically between M_{1LV} and M_{1LD} and then turns to the right and runs over the dorsal surface of the horizontal flange of M_{1LV} and M_{1RV} (hf in Fig. 3c; Pl. 2, fig. 8). This groove could well represent the course of the rectum, in which case the opening connected to it would be the anus. Such an interpretation is confirmed by the position of the opening, for the streams of water from the most median gill slits, flowing backwards parallel to the flaps, would serve to wash faeces away from the anus. The opening is, incidentally, far too large to have been a hydropore.

The only other thecal opening (mo in Fig. 1a; Pl. 2, fig. 4) lies at the anterior end, between the right and left oral appendages. The pointed plates round this opening give it the appearance of an anal pyramid, as Bather asserted (1913 : 412). However, there is no compelling reason why such a structure must have served as an outlet, and indeed, if the other openings represent gill slits and anus, then this last opening can only be the mouth, as Gislén suggested (1930 : 213). This agrees with the fact that it is much the largest opening in the theca.

An interesting peculiarity of preservation supports the present interpretation of the thecal openings. As already stated the specimens studied seem to have died by sudden burial. It is sometimes found (specimens E 23148, E 23150, E 28641) that the integuments of the theca to the right, but not to the left, of the strut are separated by a layer of rock. This is presumably because the fall of mud that killed the animal, entered the mouth before this had time to close and filled up the right-hand side of the theca. On the other hand, only a very small amount of mud could enter through the gill slits, whose flaps would shut when mud was piled on top of them.

The chambers of the theca: The features of the internal cast, integuments and external shape of *C. elizae* indicate that the theca was divided into four chambers (Fig. 4).

The existence of the first of these chambers, filling the " ankle " part of the theca, is shown by:—(a) The constant presence of a low ridge running dorso-ventrally on the inside of M_{3R}, just opposite the sharp angle in M_{5L} which separates " ankle " from " foot " (rbcr in Pl. 1, fig. 7; Pl. 2, figs. 1, 3; Pl. 3, fig. 1). (b) The presence in two specimens (rbcl in Pl. 3, fig. 1, and E 23725) of a corresponding, parallel ridge on the inside of M_{5L}. In these specimens this ridge is obviously distinct from the sharp angle just referred to, though in other specimens it is presumably inseparable. (c) The plating of the dorsal integument of the " ankle " is different from that of the " foot " (see below, p. 258). (d) The gross separation between ankle and foot visible externally. This first chamber, here called the buccal cavity, is probably homologous with the buccal cavity of chordates and the vestibule of crinoids.

Considering now the " foot " part of the theca, an undulating line can often be seen on the internal mould separating an upper from a lower part (pvl in Fig. 3b, e; Pl. 1, fig. 9; Pl. 2, figs. 2, 5). Followed from left to right (Fig. 4) the line rises from the ventral margin at point 0/1 on M_{3L}, reaches a peak at point 1, on the suture $M_{2/3L}$, descends to near the ventral border again at point 1/2 in the middle of M_{2L}, and rises to the dorsal margin of the frame at point 2, on M_{1LD}, just to the right both of the anus and of the most median gill slit. It leaves the dorsal margin at point 3, on M_{1RV} and descends vertically to point 3/4, which is just above the ventral border of the marginal frame. It then rises to point 4, near the suture M_{1RV}/M_{2R}, falls to point 4/5, situated at the " heel " in the middle of M_{2R}, and

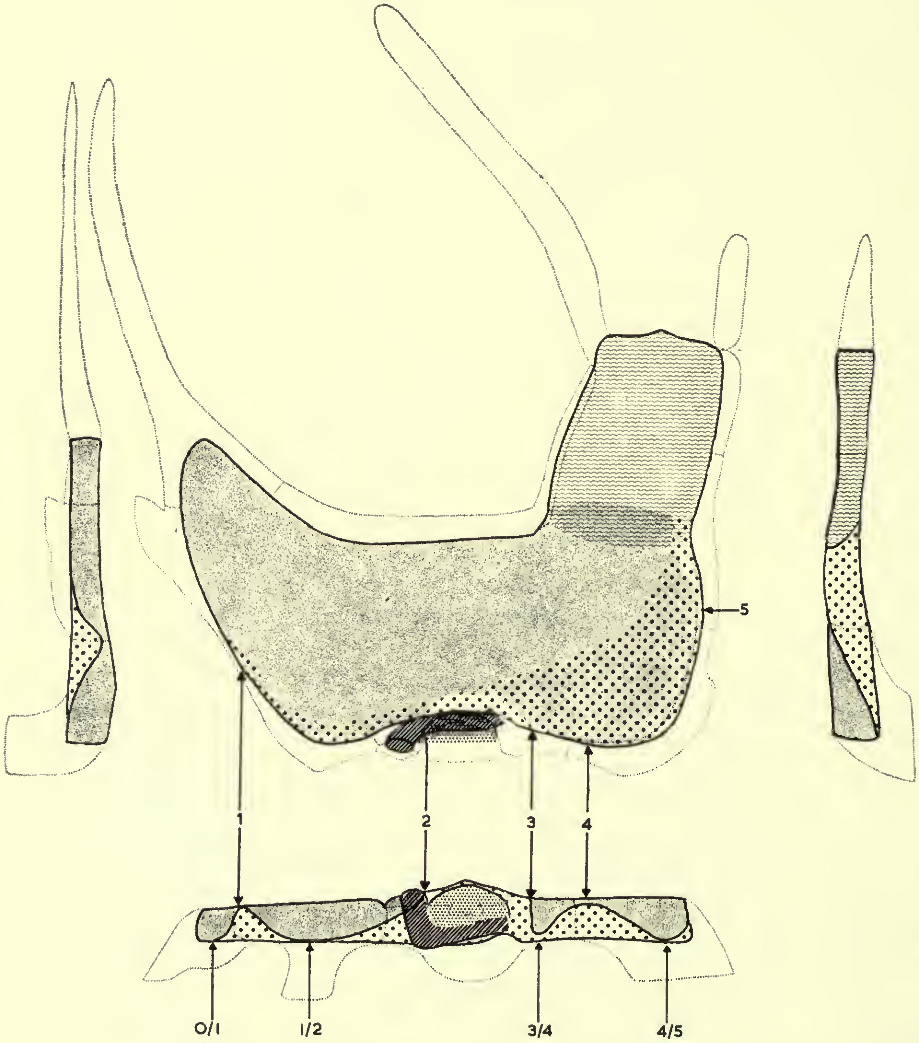


FIG. 4. *Cothurnocystis elizae.* Chambers of the theca. a. left ; b. dorsal ; c. right ; d. posterior aspects. 0/1, 1/2, 3/4, 4/5 = points where pharyngo-visceral line nears or reaches the ventral side of theca. 1, 2, 3, 4, 5 = points where pharyngo-visceral line nears or reaches dorsal side of theca. Stipple used as in Text-fig. 14.

then rises to point 5 on M_{3R}, some distance behind the posterior border of the buccal cavity. In very large specimens (Pl. 2, figs. 2, 5; Fig. 3) the area of the the internal mould above this undulating line is horizontally striated (sp). There is no trace of the lower chamber on the inside of the frame along the anterior margin of the " foot " part of the theca.

This undulating line gives the strong impression of separating two chambers and the striae above it confirm that the area dorsal to it corresponded to one and the same chamber. This upper chamber must have opened by the gill slits as is confirmed by the fact that, on the front surface of M_{1LD}, its distribution coincides with the presence of slits in the dorsal integument. The upper chamber must therefore have been the pharynx and, if so, the lower chamber would be the main visceral cavity, henceforward called the anterior coelom. The main mass of the viscera would have lain on the ventral integument somewhat to the right of, and anterior to, the stem. It is from this general region that the rectal groove emerges. The separate existence of buccal cavity and pharynx is supported by hydrodynamic considerations and by peculiarities in the plating of the integuments (see below, p. 258). The undulating line will henceforward be termed the pharyngo-visceral line.

The peaks in the pharyngo-visceral line at points 1 and 4, which are near the sutures $M_{2/3L}$ and $M_{1RV/2R}$, may be due to the optic nerves ascending almost to the dorsal side at these points, for the optic nerves of *Mitrocystites mitra* break through on to the dorsal surface at corresponding positions. This implies that at their first appearance in the cornutes the optic nerves were totally internal and came into existence before the eyes, in accordance with Studnička's theory (Walls 1942 : 126). Totally internal optic nerves would have been quite capable of functioning as light sensors. The gradual ascent of the pharyngo-visceral line between points 4/5 and 5 reflects the fact that pharynx and buccal cavity had to be connected, for obvious reasons, so that the anterior coelom in this region was pushed over to the right.

The last chamber (posterior coelom in Fig. 4; pco in Pl. 1, fig. 9; Pl. 2, fig. 1) lay just anterior to the stem and was largely bounded by skeleton. Anteriorly it seems to have had a roughly hemispherical limiting membrane (mpc in Fig. 3c) which touched the skeleton (i) at the posterior surface of M_{1LD} and M_{1RD}, and (ii) on the dorsal surface of the horizontal flanges (hf) of M_{1LV} and M_{1RV}, in the shallow, curved depression limited anteriorly by the ridge rpc (Fig. 3B, C.). The rectum (r in Fig. 3C), whose course is indicated by the rectal groove (rg), ran beneath this chamber, from right to left, and was presumably coated dorsally by the limiting membrane of the chamber. The posterior limit of the chamber would correspond more dorsally to the front of the brain. More ventrally it would correspond to the front of the vertical flanges (vf) of M_{1LV} and M_{1RV}. The posterior coelom is probably homologous to the aboral coelom of echinoderms.

To sum up, therefore, the four chambers recognizable in the theca of *C. elizae* were the buccal cavity, pharynx, anterior coelom and posterior coelom. The same chambers can be demonstrated, with variations and additions, in the other forms studied.

THE INTEGUMENTS AND MODE OF FEEDING: In very young specimens all the plates of the integuments were almost uniformly polygonal with rounded corners. In middle-sized individuals, however, there was considerable differentiation (Fig. 1a, b; Pl. 1, fig. 7; Pl. 2, fig. 3). As regards the dorsal integument, in the "ankle" region it contained polygonal plates while in most of the " foot " it contained large, circular or spheroidal plates. In the gill slit region it contained very small, rounded plates and must have been very thin. The ventral integument in middle-sized individuals contained (Fig. 1b; Pl. 2, fig. 3) polygonal plates except in a crescentic region near the anterior side of the " foot " (acp in Pl. 2, fig. 3), mainly left of the strut, where the plates were circular. In all cases circular plates touched their neighbours, if at all, at only five or six points, whereas polygonal plates touched their neighbours all round their edges. The integuments of large individuals (Pl. 1, fig. 10; Pl. 2, fig. 1) were like those of middle-sized ones except that the plates of the whole of the dorsal integument, save the small plates of the gill slit region, were large and circular. In the " foot " region, however, the plates of this integument were separated by larger spaces than those of the ankle region, which is comparable to the condition in middle-sized specimens.

The functional significance of the different sorts of integumental plates is related to the underlying thecal chambers. Wherever the pharynx touched the integuments, except in the gill-slit region, the plates tend to have larger interspaces than elsewhere. This applies both to the dorsal integument over most of the " foot " region and to the left, anterior part of the ventral integument. Such interspaces could well have contained muscles, and the corresponding parts of the integument would have been involved in pumping. The thin, small-plated integument of the gill-slit region would have been very flexible, which would clearly have made the region more efficient as a valve. The integument of the buccal cavity and the parts of the ventral integument on which the anterior coelom rested would not have been so directly involved in pumping as the parts touching the pharynx, and were consequently less well muscled.

If the pharynx was the main pumping region it would be hydrodynamically advantageous to have a valve just upstream of it, at its anterior end, to prevent forward flow. This valve, between pharynx and buccal cavity, would be the velar valve. Water may have entered the pharynx from the buccal cavity by muscular outward flexing of the pharyngeal regions of the integuments or through being driven in by cilia lining the buccal cavity and pharynx. Expulsion of water from the pharynx must have been by contraction of the muscles of the pharyngeal walls. Such contraction would tend to pull the frame inwards and to cause collapse at the middle of the anterior part of the frame, which is convex inwards. The strut in the plane of the ventral integument is perfectly placed to prevent such collapse. Phylogenetically speaking, this strut is a remnant of the completely rigid ventral shield of the Upper Cambrian *Cothurnocystis americana* Ubaghs 1963, in which there was a dorsal integument, and of the ventral skeleton of the Middle Cambrian *Ceratocystis perneri* Jaekel, where the whole theca was rigid.

C. elizae must have been a " deposit feeder ", in Hunt's terminology (1925 : 567), grazing on " the detritus deposited on the bottom and associated micro-organisms."

This is apparent since the mouth was about level with the sea bottom and since the inhalent current could only have been horizontal. The right oral appendage has sharp edges, an almost flat lower surface and a convex upper surface, and is articulated by a vertical ridge on its base to a corresponding ridge on M_{4R} (Pl. 2, fig. 4). The articulation is flanked by spaces that could well have contained muscles. This appendage seems to be adapted for waving from side to side, scraping and churning-up the surface layer of the sea bottom. The resulting suspension would be sucked in through the mouth. It is advantageous to a deposit feeder to move over the surface, grazing the bottom as *C. elizae* was probably able to do (p. 265). By contrast, *C. curvata* was probably a suspension feeder, which explains the coexistence of the two types as well as many points of difference (p. 271). In both species food particles would presumably have been carried into an oesophagus by mucus streams on the internal surface of the pharynx.

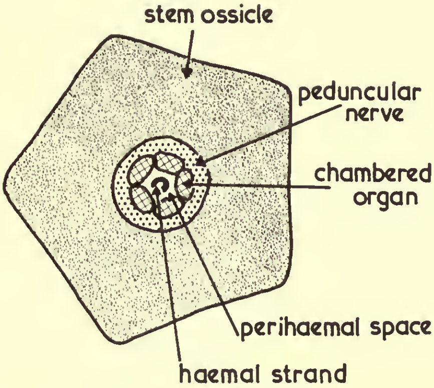


FIG. 5. Transverse section of the stem of a crinoid, based on Reichensperger (1905).

A curious feature of some young specimens is a number of specially large plates (crestal plates, cp in Pl. 1, fig. 2) in the dorsal integument. These correspond in position to a clearly marked line of plates in *Cothurnocystis americana* (Ubaghs 1963) and to the carinae on the dorsal surface of *Ceratocystis perneri*. In *C. elizae* their appearance is only sporadic and they were probably non-functional.

THE STEM: The nearest living analogue to the stem of a stylophoran is the stem of a crinoid. The probably ancestors of crinoids were the eocrinoids which include forms with distinct stems from the Middle Cambrian (*Gogia* Walcott, see Robison 1965). These are roughly contemporary with the first cornute so that, in view of the obvious gaps in the record, there is no chronological reason why the stems of crinoids and Stylophora should not be homologous.

The stem of a crinoid will now be compared with the tail of a fish. The best anatomical account of a stalked crinoid is that of Reichensperger (1905) (see Fig. 5). The central lumen of the stem contains, on the outside, the peduncular nerve, with the fibres running longitudinally. Inside this is the chambered organ, a turgid structure consisting of five adjacent tubes. Inside this is a space (here called the perihaemal space) in which lies a narrow tube called the haemal strand. The top of the chambered organ is at the proximal end of the stem. Here the five constituent tubes swell slightly and bend inwards to touch the haemal strand, so separating the perihaemal space of the stem from the thecal cavity. The haemal strand continues out of the stem into the theca, where it joins the axial organ. The haemal strand presumably functions as a blood vessel, since otherwise it is difficult to see how nutrients could reach the stem. Round the top of the chambered organ is situated the aboral nerve centre, which is the meeting-place of the aboral nerves of the theca with the peduncular nerve. The chambered organ presumably functions as the hydrostatic skeleton of the stem, helping to hold the ossicles in alignment. It is of mesodermal origin, arising as five pouches of the aboral coelom (Seeliger 1892). The origin of the aboral nervous system has never been seen, but it appears to arise later than the chambered organ.

Though never reported, muscles must exist in a crinoid stem which, in larval *Antedon*, can be bent at will (Chadwick 1907 : 37; Dimelow 1959 : 21). Hyman (1955 : 60) has pointed out that some of the " elastic " fibres in the cirri must be muscular, since these organs also can be bent at will. Elastic fibres have been reported in the stem itself, and if some of these are muscular then the nerves going from the peduncular nerves to the stem ossicles, which so puzzled Reichensperger (1905 : 30), could be their nerve supply.

The resemblances of a crinoid stem to a fish's tail are very striking. The chambered organ is like the notochord in structure, presumably in function, and to a lesser extent in origin. The peduncular nerve can be compared with the dorsal nerve cord, being applied to the surface of the chambered organ as the dorsal nerve cord is applied to the notochord. The aboral nerve centre is like the brain, for it lies at the " anterior " end of the chambered organ (= notochord) and peduncular nerve (= dorsal nerve cord) and sends out aboral (= cranial) nerves into the theca. The muscles which must exist in the stem would correspond broadly to those of the tail. The haemal strand and perihaemal space could correspond broadly to caudal artery and veins.

Furthermore the aboral nerve centre is physiologically the brain of a crinoid. Thus Langeloh (1937 : 272) showed that if it is excised the animal becomes limp and fails to carry out complicated patterns of behaviour which are otherwise instantaneous. If, however, an electric current is applied to the site of the excised centre, the appropriate reaction follows at once. The centre functions not so much in co-ordination as in summation of stimuli. In this it resembles the brain of a fish (Gray 1936; Gray & Sand 1936*a*, *b*).

A crinoid stem certainly differs from a fish's tail in a number of ways. It is pentameral, with the homologue of the notochord divided into five parts and completely surrounded by the homologue of the dorsal nerve cord. Also the stem has a calcite skeleton, has the haemal strand inside the chambered organ and is attached distally. The stylophoran stem was intermediate, for it certainly had a calcite skeleton, probably had a " haemal strand " or peduncular vessel inside the notochord, and may have been attached distally when very young. On the other hand it lacked all sign of pentamery, in common with the theca, and, at least in mitrates, had the dorsal nerve cord exclusively dorsal to the notochord. Also the segmentation of a fish's tail almost certainly corresponds with that of a stylophoran stem as regards the soft parts, but probably not with that of a crinoid stem. The correspondence of a crinoid or stylophoran stem with a fish's tail agrees with Marcus's statement (1958 : 50) that " the metamerism of the chordate trunk is fundamentally a subdivision or multiplication of the metacoel ".

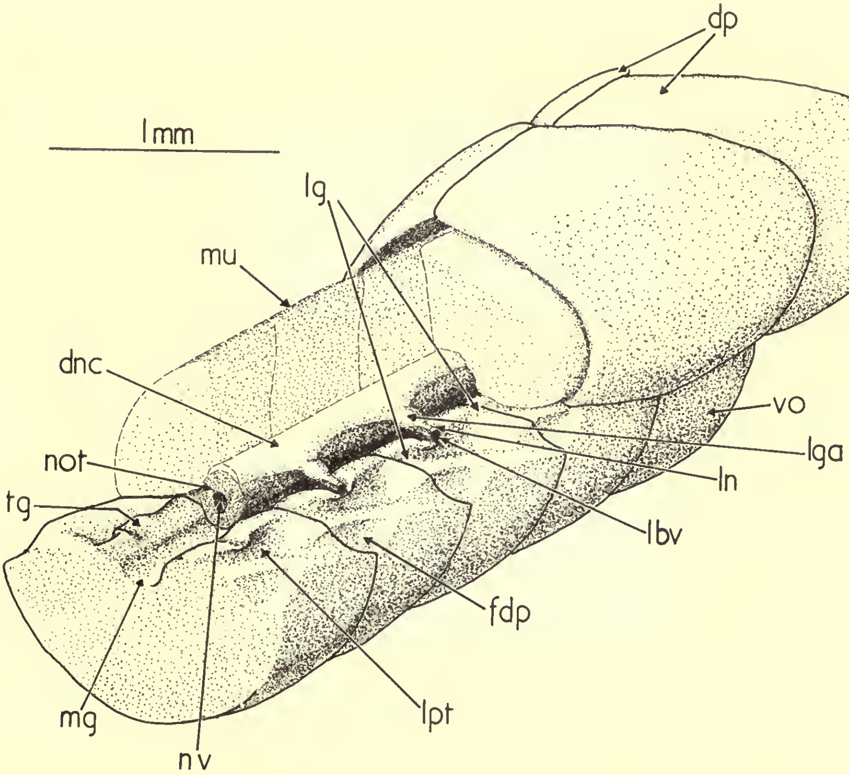


Fig. 6. *C. elizae.* Block diagram of portion of posterior stem. dnc = dorsal nerve cord; dp = dorsal plate ; fdp = facet for dorsal plate ; lbv = lateral blood vessel ; lg = lateral groove ; lga = lateral ganglion ; ln = lateral nerve ; lpt = lateral pit ; mg = median groove ; mu = muscle ; not = notochord ; nv = notochordal vessel ; vo = ventral ossicle ; tg = transverse groove.

The stem of *C. elizae* will now be described, beginning at the posterior end where the skeleton is most complicated and informative.

The posterior stem (Fig. 1, 6; Pl. 1, figs. 4, 5, 7; Pl. 2, fig. 9; Pl. 3, figs. 2, 3) consists of about 60 segments and ends abruptly. Each stem has a solid, hemicylindrical ventral ossicle (vo) and a dorsal arch formed of paired dorsal plates (dp) which meet mid-dorsally at a suture. Each dorsal arch imbricates over the front of the one behind it. Near the middle part of the posterior stem some of the ossicles project ventrally in a boss (Fig. 1c; Pl. 1, fig. 4) and the posterior faces of such ossicles are not plane, but curved about a horizontal axis. Such cylindrical surfaces would make it easier to bend the column of ventral plates vertically (Fig. 7) and it follows that the middle part of the posterior stem was vertically more flexible than the more anterior part. Towards the posterior end of the stem, the ventral bosses coalesce to form a blunt ventral keel.

The dorsal surface of each ventral ossicle is complicated (Fig. 6; Pl. 2, fig. 9). There is a median groove (mg) which runs the length of the posterior stem and connects anteriorly with the lumen of the stylocone. On each side of this groove are lateral grooves (lg) which on each ossicle are deepened into lateral pits (lpt). Outside the lateral grooves are facets for the reception of the dorsal plates (fdp). Paired transverse grooves (tg) connect the lateral pits with the median groove.

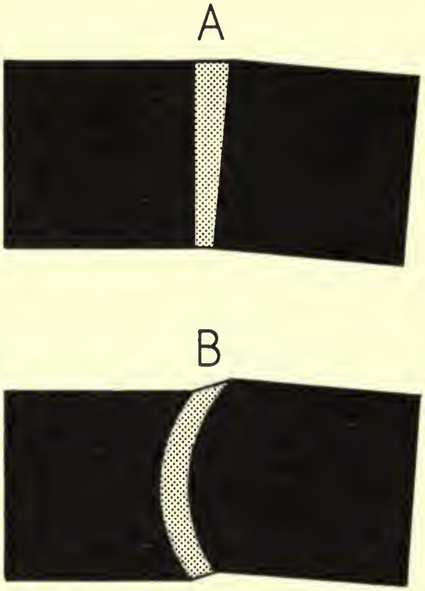


Fig. 7. A. Plane, and B. cylindrical interossicular joints. Bending at a plane joint involves compression or dilatation, or both, of the interossicular soft tissue. Bending at a cylindrical joint can occur by torsion of the soft tissue.

The median groove of *C. elizae* probably contained the chambered organ or notochord, coated, at least partially, with the peduncular nerve or dorsal nerve cord. By analogy with the mitrates the nerve was perhaps restricted to the dorsal surface as shown in Fig. 6. The imbricate dorsal plates show that the posterior stem could flex upwards. For this, muscles (mu) would be needed. They would lie in the space between dorsal plates and ventral ossicles and would be seated in the lateral grooves. They were probably divided into muscle blocks, the divisions between which, by analogy with *C. curvata* and the mitrates, would correspond to the transverse grooves. Muscles would need nerve and blood supply. The transverse grooves may possibly mark the course of lateral blood vessels connected with a central peduncular blood vessel (nv in Fig. 6) in the notochord that was homologous with the haemal strand of crinoids. Along the dorsal surface of the lateral blood vessels, by analogy with the mitrates, lateral nerves may have run. The extensor force opposing the muscles was probably due to the column of ventral plates which may have been elastic like a recent crinoid stem when wet (personal observation). The abrupt end of the posterior stem is of some interest. It strongly suggests that at some stage in the life history the stem extended posterior to what now remains. Indeed, it is possible that when very young the animal was attached by a holdfast, like a crinoid, from which it later broke free. An abrupt end to the stem is also found in all the other forms studied.

Ubaghs (1961*b*) has interpreted the structures of the posterior stem of both cornutes and mitrates as representing a water vascular system (median groove = main water vessel; lateral grooves = lateral water vessel; lateral pits = sites of tube feet; dorsal plates = cover plates; stem as a whole = arm of asterozoan). This seems quite unacceptable for reasons which will be set out in detail after the mitrates have been discussed.

The medial stem (Fig. 1; Pl. 1, figs. 3, 4, 7) corresponds to two segments and is made up of the stylocone (stc) ventrally and two pairs of plates dorsally. The large anterior cavity of the stylocone connects with the median groove of the posterior stem and is flanked by two pairs of lateral pits, with transverse grooves leading to them. The stylocone resembles two fused ventral posterior stem ossicles, with which it is serially homologous. It is also presumably homologous with the paired ventral plates of the anterior stem. It served as a rigid barrier to separate the powerful muscles of the anterior stem, which moved the stem sideways, from the muscles and ventral ossicular column of the posterior stem, which moved it up and down. If the muscle blocks of the posterior stem and anterior stem had formed continuous columns, separated only by myocommata, then contractions of the anterior muscles would have produced functionally irrelevant elongations of the more anterior muscle blocks of the posterior stem on one side only.

The anterior stem is offset downwards from the theca (Fig. 1b, c), so that its median ventral line is lower than the ventral surface of the latter. It consists of five rings of plates (cf. Ubaghs 1961*a*; Caster 1952) enclosing a large lumen. Each ring has four plates—left, dorsal and ventral and right, dorsal and ventral—denoted by D_{nL}, VS_{nL} and D_{nR} and VS_{nR} in ring $_{n}$. The dorsal plates are much smaller than the ventral plates. Each one is apposed to its antimere at the median line and imbricates below the corresponding ventral plate ventrally. The dorsal plates are evidently serial homologues of those of the medial and posterior stem.

The ventral plates of the anterior stem are crescentic in anterior or posterior aspect. They are therefore thinner near their dorsal and ventral ends than near the middle. The posterior surface is always almost plane. The anterior surface is either almost plane or produced into an admedian imbrication flap (if in Pl. 1, fig. 10) which is not developed near dorsal and ventral ends of the plate.

The length of a ventral plate, measured along the length of the stem and omitting the imbrication flap, is greater near the mid-line than more laterally (Pl. 1, fig. 10). Successive pairs of ventral plates touched each other ventrally, without imbrication, and almost touched dorsally. There would therefore, when the anterior stem was held straight, have been gaps between successive plates at right and left, and these would have allowed lateral flexing.

The first pair of ventral plates (VS_{1L}, VS_{1R}) fitted into a reception groove in M_{1RV} and M_{1LV} (reg in Fig. 3d). The gap between the corresponding dorsal plates (D_{1L}, D_{1R}) and the arch formed by M_{1LD} and M_{1LD} and M_{1RD} was filled by a pair of dorsal plates (D_{OL} and D_{OR}) with no ventral plates corresponding.

The skeleton thus shows that the anterior stem was adapted to flex sideways but not up and down, and the way the specimens are preserved confirms this. The anterior stem is found flexed in any position from extreme right to extreme left as it lay at the moment of burial (e.g. Pl. 1, figs. 4–7). The soft parts of the anterior stem must have consisted mainly of powerful muscles, presumably divided into segmental blocks. An anti-compressional structure (notochord or chambered organ), which would have maintained the alignment of the skeletal rings, is likely to have existed. It would be a forward continuation of the notochord of the posterior and medial stem, would contain the peduncular blood vessel and would be coated by the peduncular nerve or dorsal nerve cord. Segmental nerves and blood vessels to the muscles must also have been present.

THE BRAIN: By analogy with a crinoid the aboral nerve centre or brain of *Cothurnocystis elizae* must have occupied a prominent basin (cerebral basin, ceb in Fig. 3) excavated in the postero-ventral faces of M_{1RV} and M_{1LV} where the stem joins the theca (Pl. 2, fig. 6).

A median notch (nmln) in the dorsal edge of plates M_{1RV} and M_{1LV} leads to two grooves (gmln), running outwards and downwards, on the anterior face of the vertical flange (vf) of these plates (Fig. 3, Pl. 2, fig. 8). The left groove can sometimes be followed to the floor of the rectal groove (Pl. 2, fig. 7). The right groove is somewhat shorter, probably because the structure that it carried left the skeleton earlier. To right and left of the median notch are two triangular depressions (pbd) excavated in the dorsal surface of M_{1RV} and M_{1LV}.

The soft structures indicated by the notch, grooves and depressions, since they came off the brain, were probably nervous. The depressions probably carried ganglia, corresponding to the pyriform bodies (pb in Figs. 19a, 27a) of mitrates. The grooves probably carried nerves (median line nerves). Since the left one passed under the rectum this, at least, was more ventral than any nerves of which there is evidence in mitrates, with the possible exception of the nerves n_0. The optic nerves, whose possible terminations have been indicated above, presumably left the brain more dorsally, through the notch, and passed dorsal to the rectum.

ONTOGENY: Very small specimens much resemble adults. At a length (measured from the stem base to the anterior end of M_{5L}) of 6 mm., gill slits already existed and extended back to the anus, as in the adult. Their number could not be determined. The smallest specimens (e.g. Pl. 2, fig. 4) do not have the stem offset ventrally with respect to the theca and lack ventral spikes, which first appear on the sides of the marginals. The number of rings in the anterior stem is smaller (only 3 in Pl. 1, fig. 3) and the number of ossicles in the posterior stem is about fifteen, as opposed to about 60 in the adult. The smallest specimens have the ventral mouth frame oblique to the "ankle" region, the left end being more anterior than the right.

Posture and movement: The bizarre shape of *C. elizae* calls for a reconstruction of its habits (cf. Bather 1913 : 415; 1928; Gislén 1930 : 217).

As Bather and Gislén said, the theca must have rested on the sea bottom, supported on the ventral processes and anterior appendages, and with the dorsal surface upwards. The right oral appendage was motile (see above, p. 259). Of the remaining fixed processes and appendages, four are roughly parallel to each other (the left-hand spikes S_{1L} and S_{2L}, and the left oral and left appendages), whilst the remaining one (the right-hand spike S_R) is perpendicular to the others, cf. Fig. 1b. In life the anterior appendages would have dipped down anteriorly into the mud. The spikes S_{1L} and S_{2L} (Pl. 1, fig. 6) have sharper points anteriorly than posteriorly. S_R is always flat-bottomed and S_{1L} sometimes so.

When at rest on the bottom the theca could not have moved anteriorly, for the appendages and left-hand processes would have been forced into the sea-floor. This is the more true since S_R, which ends ventrally in a flat suitable for resting on the sea-floor, and the anterior stem, which is distinctly offset ventrally, would have raised the posterior part of the theca. The theca appears to be adapted to slip posteriorly in a direction parallel to the two fixed appendages (lap and loap) and the two left-hand spikes (S_{1L} and S_{2L}), and perpendicular to the right-hand spike (S_R). The obvious motility of the stem supports Gislén's suggestion (1930 : 217) that it was the main organ of movement. It is suggested here that it acted by pulling the theca *backwards* across the sea floor in the direction indicated above. The sea floor would be gripped by the ventral bosses on the posterior stem and by bending the tip downwards. The power stroke would be applied by flexing the anterior stem to left or right as appropriate.

Such a mode of operation explains: 1. the specialization of the parts of the stem for different planes of flexion; 2. the exact forms of the spikes and fixed appendages of the theca, which would serve admirably to prevent yawing and also to prevent forward movement during the return stroke of the stem; 3. the concentration of ventral bosses for gripping the sea-floor, and curved interossicular surfaces for downward flexion in the middle and posterior parts of the posterior stem.

Many features show that, when resting on the sea-floor, the usual direction of movement of the other forms studied was also backwards.

b. *Cothurnocystis curvata* Bather 1913

Systematic position: See *C. elizae*. Both species belong to the Family Cothurnocystidae. Professors Caster and Ubaghs are about to create a new genus for *C. curvata* (personal communication). This is certainly justified.

Occurrence: As *C. elizae*.

Material: About 40 specimens, collected by the Gray family and preserved in the British Museum (Natural History). The registration numbers are as follows: E23128, E23132, E23142, E23151, E23160, E23165, E23168, E23173, E23701, E 23715, E 23728, E 23738, E 23739, E 23744, E 23748, E 23750–1, E 23754, E 23756, E 23758, E 23767, E 28427, E 28551, E 28552, E 28555, E 28574, E 28609, E 28617, E 28630, E 28633–4, E 28647–50, E 28652–3, E 28655, E 28661–2, E 28665. Also G.S.M. 60839 from the Geological Survey & Museum, London and 1958.1.252 from the Royal Scottish Museum, Edinburgh.

General shape and plate nomenclature: The general shape of the theca (Fig. 8a–e) is much like *C. elizae* but more symmetrical. The most obvious difference is the presence of only one oral appendage—a fixed structure probably corresponding to the left oral appendage of *C. elizae*. In addition the anterior part of the theca is convex upwards, whence the specific name. The marginal plates are numbered according to the scheme used in *C. elizae*, but homologous plates do not always bear the same numbers, as the table below shows.

C. curvata

Bather 1913	Present notation	Homologous plate in *C. elizae*
Not shown	M1LD	M1LD
5	M1LV	M1LV
6 and 7	M2L	M2L
	—	M3L
8	M3L left appendage	M4L left appendage
	M4L	—
9, 10 and 11	M5L anterior strut plate	M5L anterior strut plate
Not shown	right appendage	left oral appendage
	—	M6L
Not shown	M1RD	M1RD
4	M1RV	M1RV
3	M2R	—
	M3R	M2R
2	M4R bucco-pharyngeal plate	M3R (bucco-pharyngeal plate bearing bucco-pharyngeal ridge)
1	M5R	M4R
	—	M5R

M3L, M5R, M6L and the right oral appendage of *C. elizae* are not represented in *C. curvata*. M2R, M4L of *C. curvata* are not represented in *elizae*.

Ventral spikes were present on M2R, M3R and sometimes M4R (see Pl. 3, fig. 7), and on M2L. These spikes are denoted respectively as S1R, S2R, S3R and SL.

Thecal openings: The branchial slits (Fig. 9; Pl. 3, figs. 2, 3, 4, 7) are situated much as in *C. elizae* but number about 40 and differ in structure. The slits are separated by chevron-shaped plates (interbranchial chevrons, ibc in Fig. 9) each of which fits accurately against its neighbours. The low crest of the chevron (cr) points outwards and may represent a suture, for it often fractures. Each interbranchial chevron has grooves in its sides just above the ventral margin (arcuate grooves, arg in Fig. 9). These grooves end anteriorly and posteriorly as the cavities of hollow processes (anterior and posterior excavate processes, aep, pep in Fig. 9).

Most of the ventral surface of the chevron is occupied by a ventral groove (vg) which is widest beneath the crest of the chevron. The rest of the ventral surface is occupied by the ventral walls of the arcuate grooves except for anterior and posterior semicircular tabulate areas at the tips of the chevron.

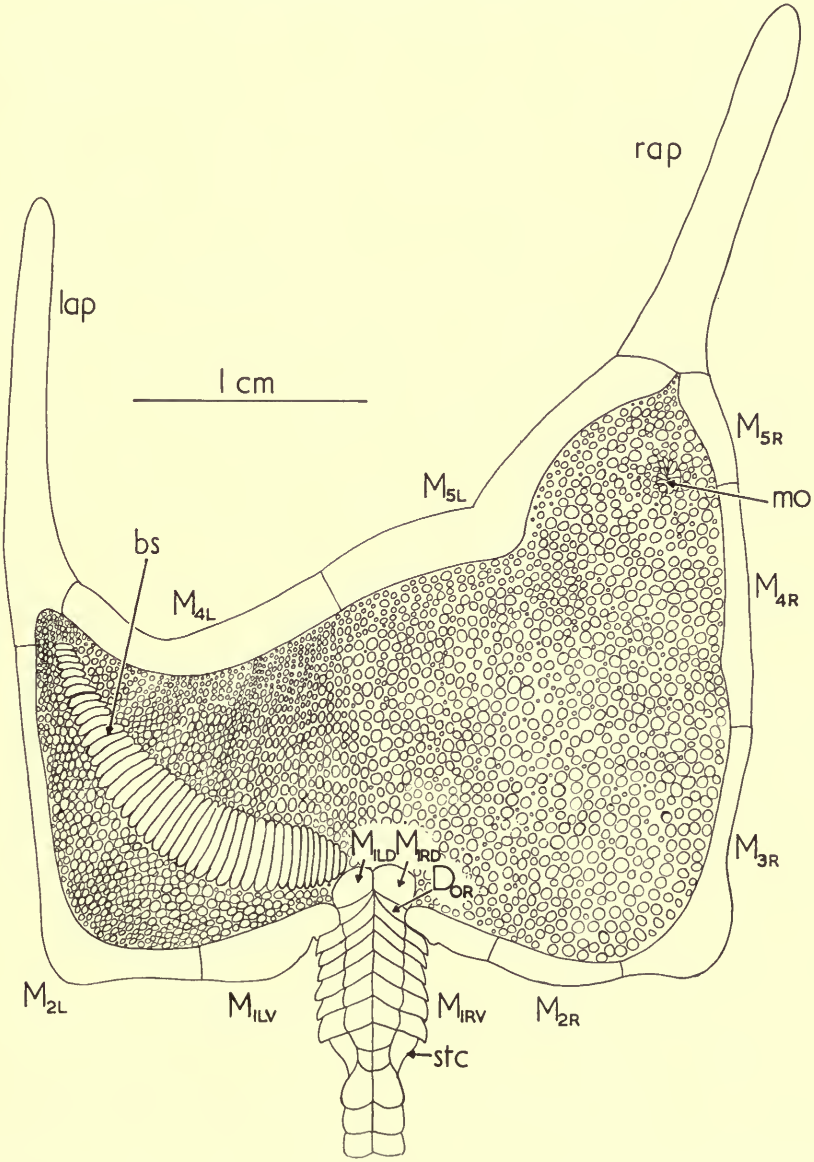

rap
lap
1 cm
M5R
M5L
mo
bs
M3L
M4L
M4R
M3R
M1LD
M1RD
DOR
M2L
M1LV
M1RV
M2R
stc

FIG. 8. *Cothurnocystis curvata.* Reconstruction of external features. a. dorsal; b. ventral c. anterior ; d. posterior ; e. left ; f. right aspects. bs = branchial slit ; lap = left appendage ; rap = right appendage ; stc = stylocone ; str = strut.

The branchial complex almost certainly acted as an outlet valve. It was mounted in a flexible integument. When the pressure was high beneath this integument the complex would belly out, the chevrons would separate from each other and water would escape. When the internal pressure consequently decreased the integument would deflate, the chevrons would clap together and water would be unable to enter. The crests of the chevrons would coincide with the line of greatest

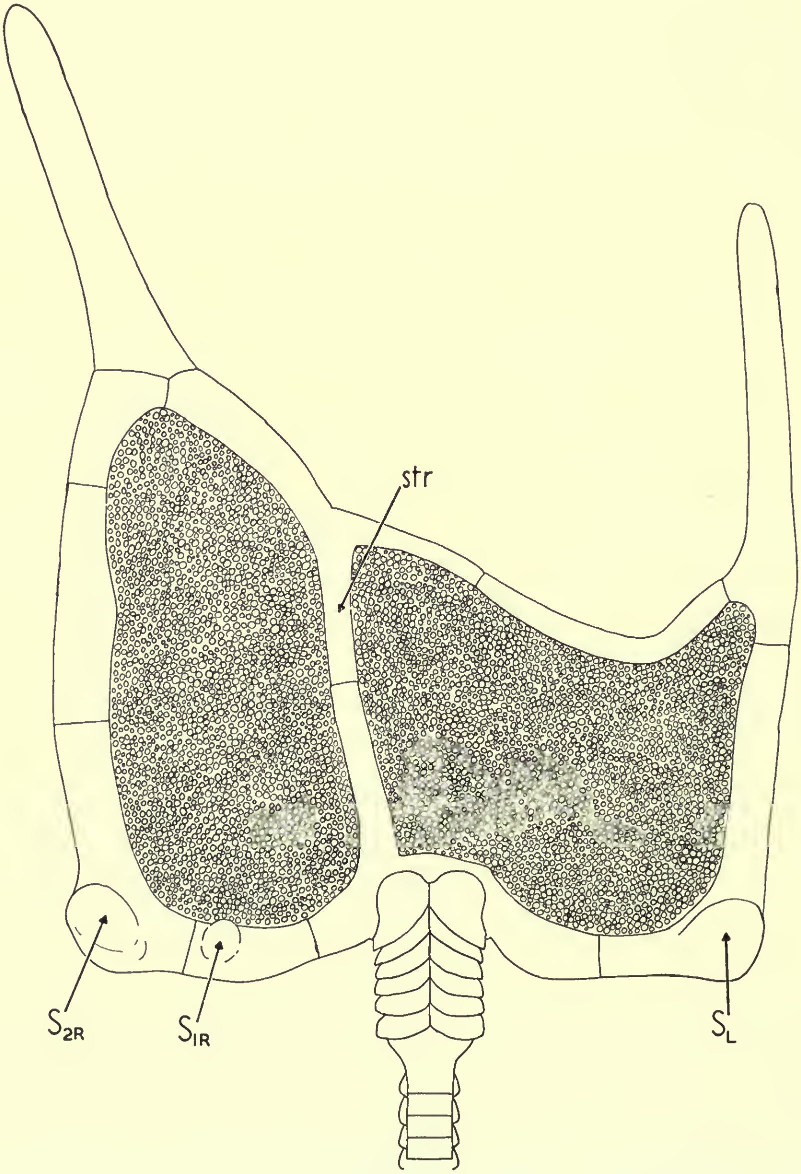


FIG. 8b.

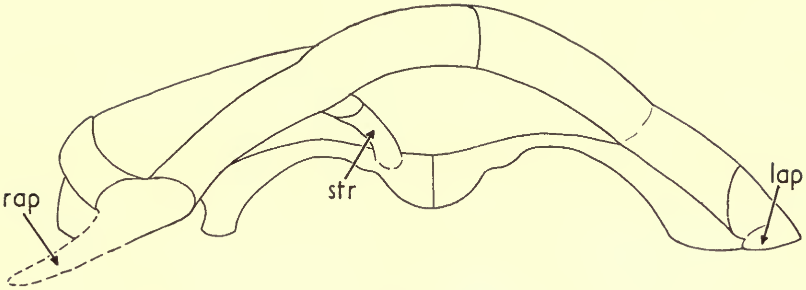


FIG. 8c.

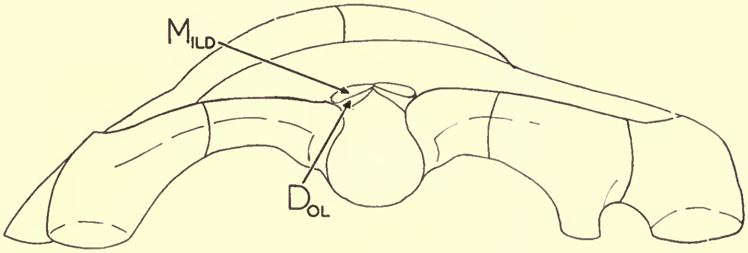


FIG. 8d.

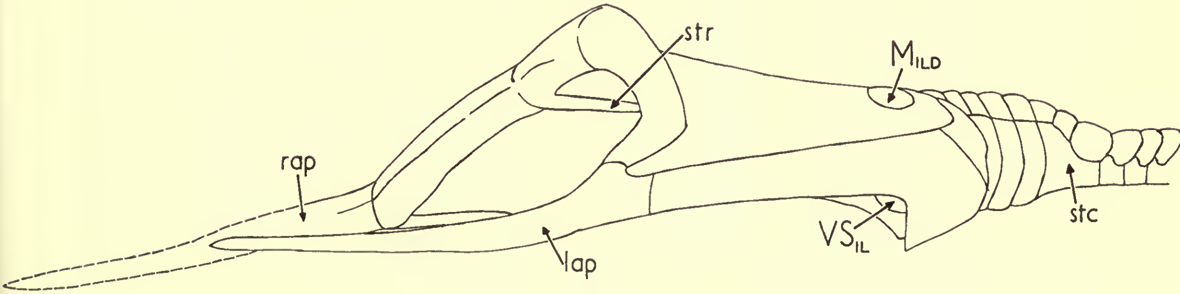

str
M_{ILD}
rap
stc
VS_{IL}
lap

FIG. 8e.

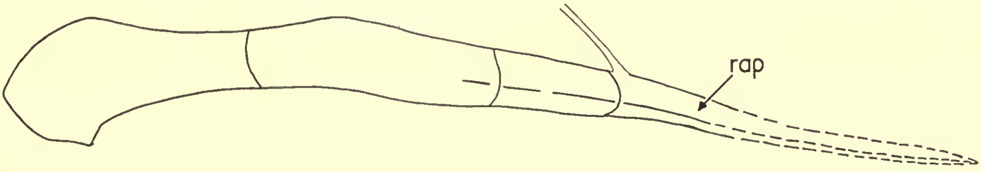


FIG. 8f.

stretching of the integuments, and this would increase the efficiency of the valve mechanism.

Each arcuate groove was probably filled with connective tissue, which may have projected slightly out of the groove when the chevrons were separate. It would consequently press against the contents of the neighbouring arcuate groove when the

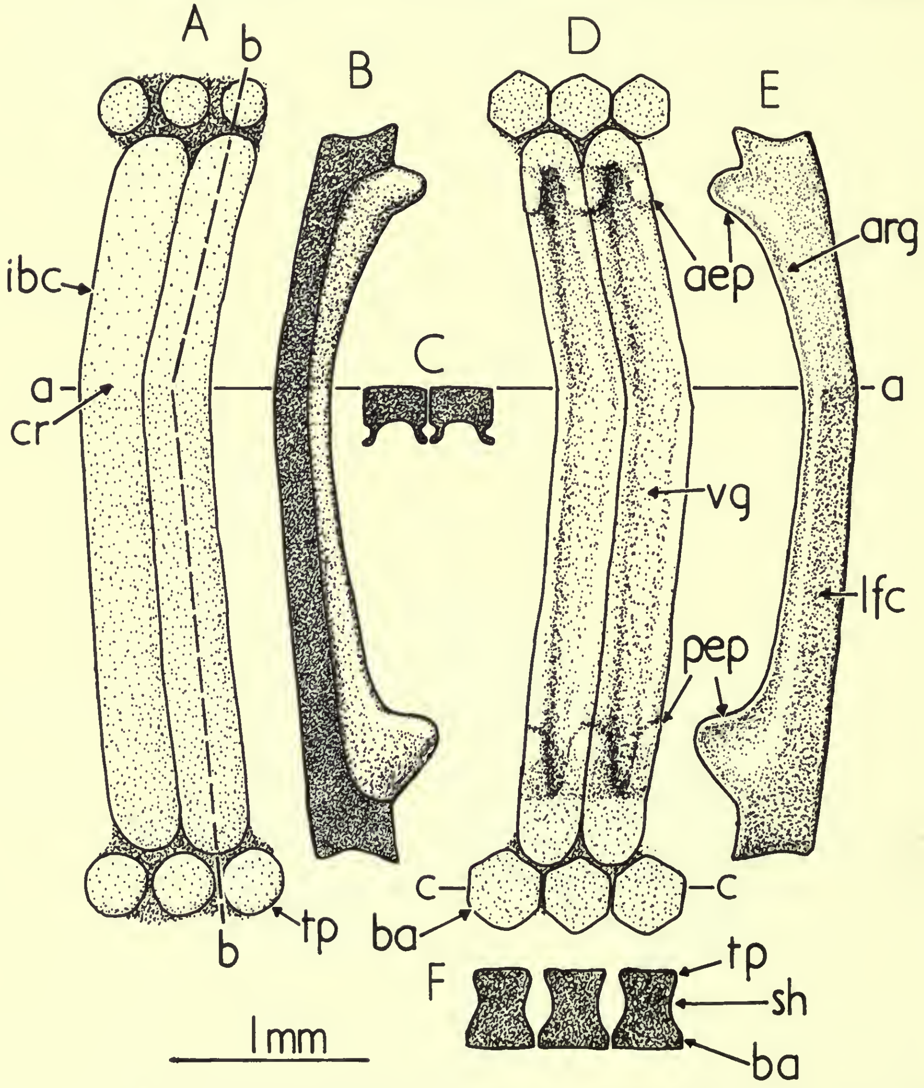


FIG. 9. *C. curvata.* Branchial skeleton. A. External aspect ; B. longitudinal section through b-b ; C. transverse sections through a-a ; D. internal aspect ; E. left lateral aspect ; F. Section through plates of integument c–c. aep = anterior excavate process; arg = arcuate groove ; ba = base ; cr = crest ; ibc = interbranchial chevron ; lfc = lateral facet ; pep = posterior excavate process ; sh = shaft ; tp = top ; vg = ventral groove.

chevrons clapped together. This would provide an excellent seal which would increase the efficiency of the valve. The facts that: (i) the length of an arcuate groove coincides exactly with the extent to which neighbouring chevrons touch each other, (ii) the edges of an arcuate groove match exactly against those of its neighbour, (iii) the ventral positions of the grooves coincide with the parts of the chevrons that would first come together on deflation, strongly confirm this interpretation.

By comparison with *C. elizae* each chevron represents the fusion of adjacent halves of neighbouring anterior and posterior u-plates. The presumed crestal suture of *C. curvata* represents the articulation between anterior and posterior u-plates of *C. elizae* and also a corresponding suture through the branchial slits of *Ceratocystis perneri*. The branchial valve mechanism of *C. elizae* depended on the bellying-out of the integuments under pressure, the bending of the frames of the slits, and the flexibility of the flaps. The branchial valve mechanism of *C. curvata* depended only on the bellying-out of the integument.

There is no external anus in *C. curvata* (Fig. 8a; Pl. 3, figs. 9, 10). An obvious rectal groove (rg in Fig. 11a; Pl. 3, fig. 5) runs across the floor of the posterior coelom but, instead of opening directly to the outside, joins a distal rectal canal (drc in Fig. 11a; b; Pl. 3, fig. 9) in M_{1LD} running anteriorly and dorsally. This canal leaves M_{1LD} where only a small stretch of integument separates it from the most median interbranchial chevrons. The anus must therefore have been internal, opening into the most median branchial slits, downstream of any food-collecting surface inside the pharynx.

The outlet current from the gill slits of *C. curvata* would be perpendicular to the integument, instead of horizontal and backwards as in *C. elizae*. A very close association of branchial slits and anus would therefore be advantageous. This close association proves that the distal rectal canal was indeed an outlet and confirms the identification of the anus in *C. elizae*.

The mouth was surrounded by pointed plates, as in *C. elizae*, but was dorsal in position. This involves no difference in the " connections " with the surrounding skeleton, for even in *C. elizae* a lower lip separates the mouth from the nearest parts of the marginal frame (M_{6L} and M_{5R} in *C. elizae*).

The dorsal position of the mouth shows that *C. curvata*, unlike *C. elizae*, was a suspension rather than a deposit feeder. This explains a number of other differences from *C. elizae*, viz: 1. the absence of the right oral appendage, which in *C. elizae* was specialized in connection with deposit feeding, 2. The narrowness of the rectal groove, which would not need to carry much mineral detritus. 3. The possible loss of powers of movement in the adult (see p. 277), since there would be no need to graze the sea floor.

THE CHAMBERS OF THE THECA: A buccal cavity corresponding to that of *C. elizae* is indicated by: (i) the gross separation of " ankle " and " foot " region, visible externally, (ii) the presence of a dorso-ventral ridge (rbcr) on the inside of M_{4R} (Pl. 3, figs. 2, 7), just opposite the sharp angle (rbcl) in M_{5L} between " foot " and " ankle " regions, (iii) gaps between the attachment facets of dorsal and ventral integuments visible on the internal cast both to right and left of the " ankle " region.

These gaps are widest in the middle of the region and diminish and disappear both anteriorly and posteriorly (Fig. 10a, b, d; Pl. 4, figs. 2, 3). They suggest a definite chamber between the integuments in this area.

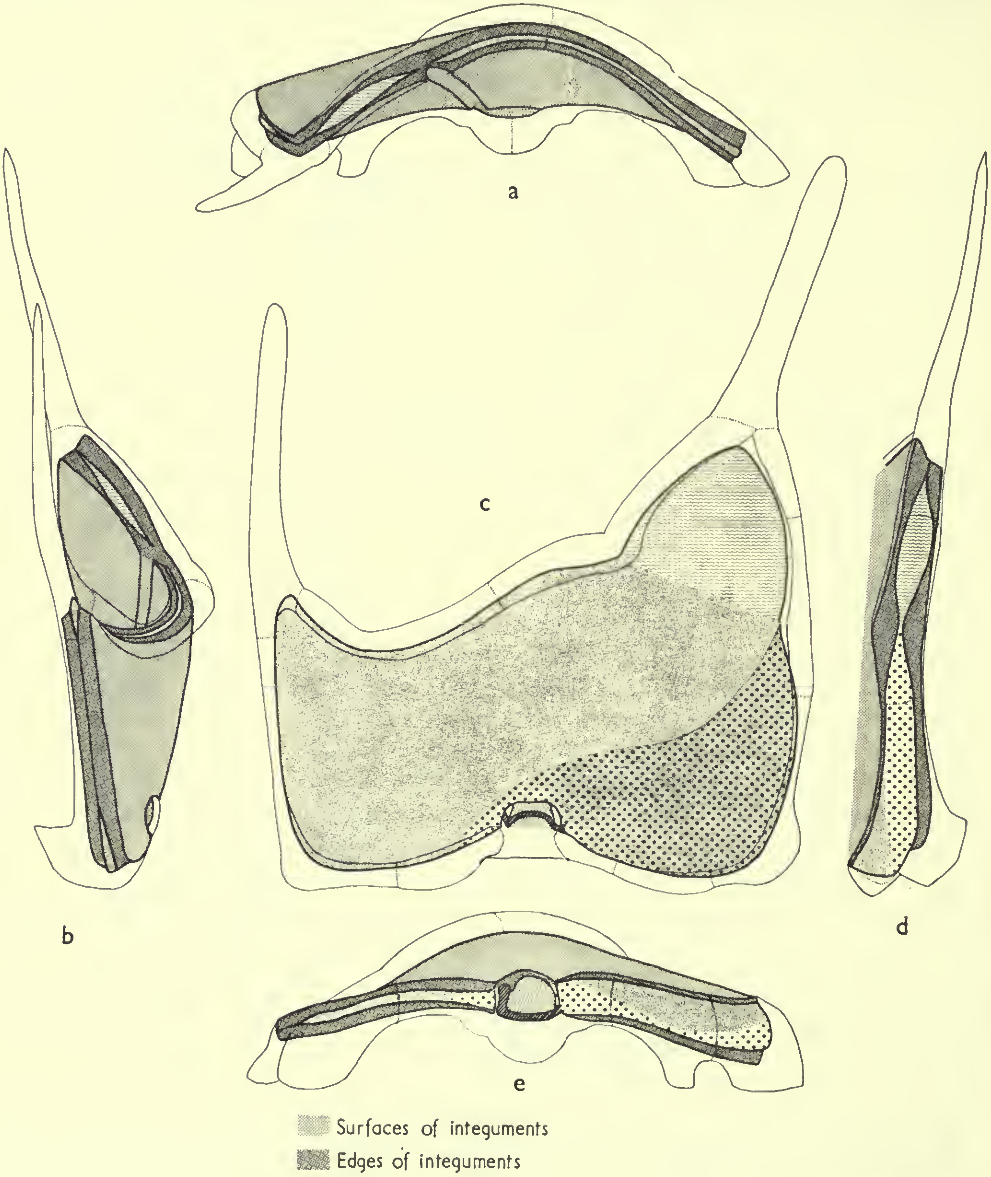

a
c
b
d
e
Surfaces of integuments
Edges of integuments

Fig. 10. *C. curvata*. Chambers of theca. a. anterior; b. left; c. dorsal; d. right; e. posterior aspects. Skeleton assumed to be transparent and, except in 10c, the integuments assumed to be opaque. Stipple of chambers as in Text-fig. 14.

The posterior coelom (pco in Fig. 11a; Pl. 3, figs. 2, 5) shows more clearly than in *C. elizae*. It is floored by the dorsal faces of M_{1LV} and M_{1RV}, roofed over by the ventral faces of M_{1LD} and M_{1RD} and defined antero-ventrally by antero-ventral processes (avp) of the latter, which rest directly on M_{1LV} and M_{1RV}. The posterior coelom lay in front of the brain and the rectum ran in the rectal groove (rg) beneath it.

The positions of anterior coelom and pharynx cannot be deduced directly from the superficial internal anatomy. As in *C. elizae*, however, the anterior coelom probably lay mainly in the posterior, right-hand part of the theca, since the rectum entered the posterior coelom from this region and the space between the integuments is much deeper to the right of the stem than to the left (Fig. 8d).

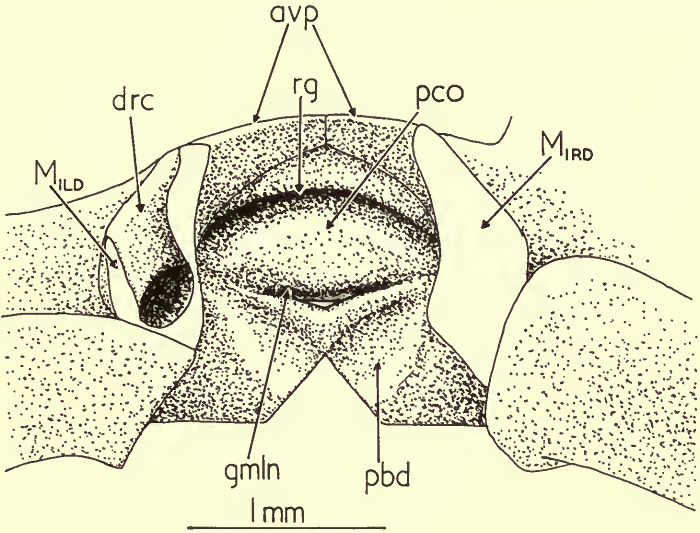


FIG. 11. *C. curvata*. Structure of region just anterior to stem. a. dorsal aspect, with most of M_{1L} and RD removed; b. anterior; c. posterior aspect. avp = antero ventral processes of M_{1L} and RD; ceb = cerebral basin; cmln = canal for median-line nerves; drc = distal rectal canal; gmln = groove for median-line nerve; pbd = depression for pyriform bodies; pco = posterior coelom; reg = reception groove for anterior stem; rf = rectal foramen; rg = rectal groove.

THE INTEGUMENTS: The plates of the integument (Fig. 9F) consist of a polygonal base (ba) internally, with a process arising from it. This process may have a constricted shaft (sh) and an expanded top (tp), or it may be hemispherical or have some intermediate shape. The polygonal base is everywhere in contact with its neighbours.

Dorsal and ventral attachment facets (uiaf and liaf) for the integuments, in most places separated by a space of varying depth, existed on the inner faces of the marginal plates (Fig. 10; Pl. 4, figs. 2, 3, 5, 6, 8).

Differentiation of the integument plates is less marked than in *C. elizae*. The plates of the ventral integument are smaller than those of the dorsal integument.

Plates with hemispherical processes are commonest in the posterior right-hand corner of the theca.

The spaces between neighbouring processes probably contained muscle. The shortness of the processes in the posterior right-hand corner therefore suggests that the plates here were less involved with pumping than elsewhere. This can be related to the probable position of the anterior coelom.

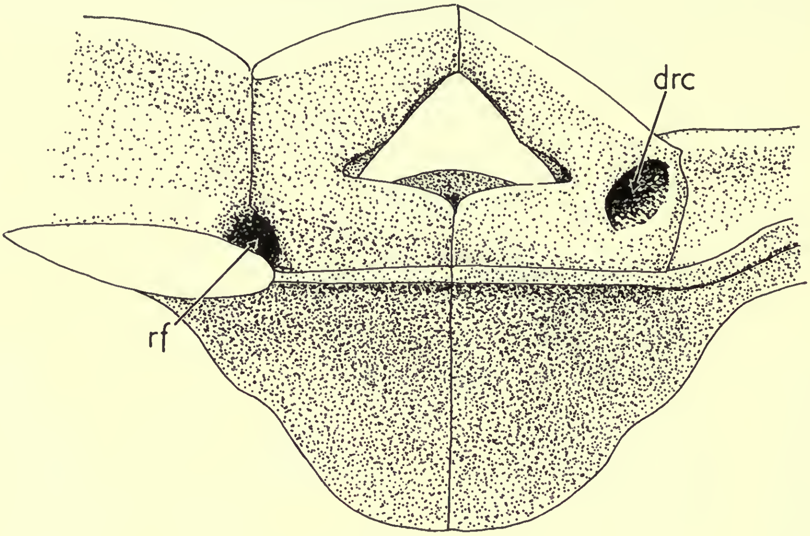


Fig. 11b.

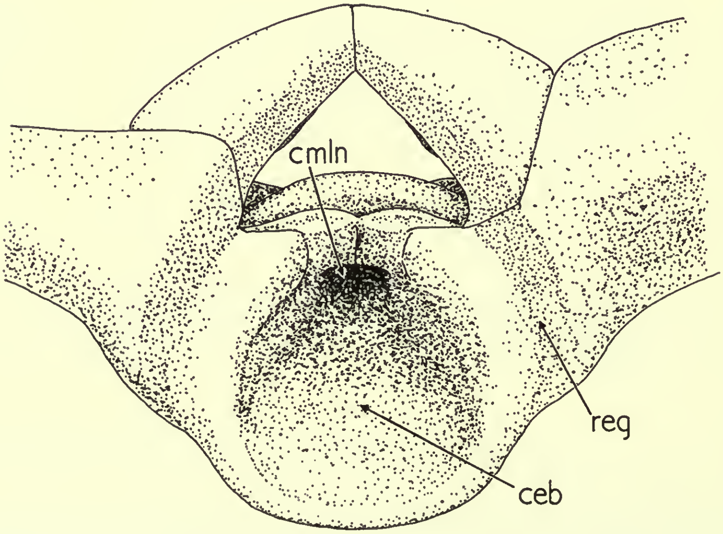


Fig. 11c.

THE STEM: The posterior stem is incomplete in all the larger specimens studied. In E 28661, whose maximum width across the theca was 18 mm., it must have contained more than sixteen segments. The number of segments increased in ontogeny for in E 28552 (thecal width = 6·5 mm.) there are only nine segments in the whole posterior stem. As in *C. elizae* the stem, when complete, seems to have ended abruptly.

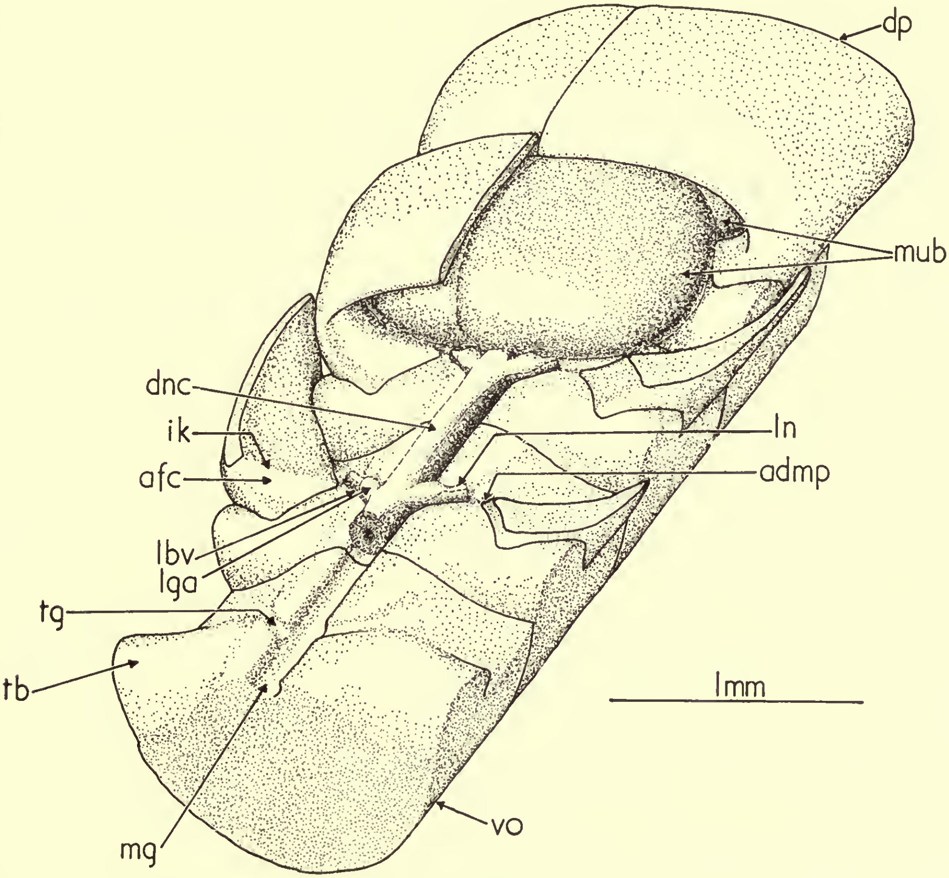


FIG. 12. *C. curvata.* Block diagram of portion of posterior stem. admp = admedian process of dorsal plate ; afc = anterior facet of dorsal plate ; dnc = dorsal nerve cord ; dp = dorsal plate ; ik = internal keel of dorsal plate ; lbr = lateral blood vessel ; lga = lateral ganglia ; ln = lateral nerve ; mg = median groove ; mub = muscle blocks ; tb = transverse buttress ; tg = transverse groove ; vo = ventral ossicle.

The structure of individual segments is basically (Fig. 12; Pl. 4, figs. 1, 4) as in *C. elizae*. There was a hemicylindrical ventral ossicle (vo) and a pair of dorsal plates (dp). The dorsal surface of the ventral ossicle carried a median groove (mg) which gave rise to a pair of transverse grooves (tg) running obliquely backwards. Unlike *C. elizae*, the anterior half of the dorsal face of each ventral ossicle carried paired, hemicylindrical, transverse buttresses (tb). The dorsal plates were thicker than in *C. elizae* and there is an internal keel (ik) separating an anterior internal facet (afc) from the rest of the internal surface of the plate. The internal keel ends ventrally in an admedian process (admp). The interface between a ventral ossicle and a dorsal plate is of large area and complicated shape, straddling the transverse buttress and part of the dorsal surface of the same ossicle behind the buttress.

As regards interpretation, it is clear, firstly, that the dorsal plates, because of their complicated ventral articulation, could not have opened outwards as Prof. Ubaghs' hypothesis would require. Secondly, the space between dorsal plates and ventral ossicles, which would be largely filled with muscle, is partially subdivided by the admedian processes and internal keels of the dorsal plates. This partial subdivision probably indicates the division between muscle blocks (mub) as shown in Fig. 12. Thirdly, the transverse grooves, which probably carried lateral blood vessels (lbv) ventrally, with lateral nerves (ln) and ganglia (lga) overlying, must have run between the muscle blocks if these were arranged as suggested. In this they resembled the ganglia and probable lateral blood vessels of mitrates. The posterior stem was probably stiffer in life than that of *C. elizae* for it is relatively stouter, the faces between the ossicles are all exactly plane, and there was relatively less space for muscles.

The medial stem of *C. curvata* differs from that of *C. elizae* in having three segments, indicated by three pairs of dorsal plates, instead of two. It also has a very abrupt posterior taper, especially dorsally.

The anterior stem is offset ventrally to the theca to an even greater degree than in *C. elizae* (Fig. 8d). It has about six segments, each containing right and left, dorsal and ventral plates as in *C. elizae.* All the plates of a ring imbricate everywhere beneath the corresponding plates of the ring next in front. This would give flexibility dorso-ventrally as well as laterally. The anterior ventral plates (VS$_{1L}$ and VS$_{1R}$) fit dorsally in a reception groove in M$_{1LV}$ and M$_{1RV}$. More ventrally they overlap these two plates, which again would allow vertical flexion. Between the dorsal plates D$_{1L}$ and D$_{1R}$ and M$_{1LD}$ and M$_{1RD}$ two small triangular plates (D$_{0L}$ and D$_{0R}$) are inserted as in *C. elizae,* without ventral plates corresponding.

The anterior stem would need some anticompressional structure (notochord or chambered organ) to prevent telescoping, since compressional stresses would be taken up by the skeleton even less than in *C. elizae.* A nerve cord, powerful muscles, presumably in blocks, and a blood supply must also have existed.

The brain: The brain is much like that of *C. elizae.* It was contained in a cerebral basin (ceb in Fig. 11c; Pl. 3, fig. 8) excavated in M$_{1LV}$ and M$_{1RV}$. The median line nerves left the brain in a canal (cmln in Fig. 11c) which bifurcates away from the brain and leads to two grooves (gmln in Pl. 3, fig. 5). There are triangular depressions (pbd) for the pyriform bodies.

Posture and movement: There is no doubt that *C. curvata* lived with the dorsal side uppermost since, as in *C. elizae,* all the openings are dorsal and all processes are ventral.

The habitual direction of movement must have been backwards as in *C. elizae.*

This is shown by the anterior appendages, which dip downwards anteriorly, and the spikes S_{1R}, S_{2R}, S_{3R} and S_L which are truncated by oblique planes, dipping downwards anteriorly (Fig. 8e, f). The theca is more symmetrical than in *C. elizae*, however, and the habitual direction of movement, parallel to the anterior appendages, must have been more directly backwards.

The stem cannot have acted exactly as in *C. elizae*, for the anterior stem could flex up and down, as well as sideways, and the posterior stem was probably relatively stiff. The prominent anterior appendages would have prevented yawing, and suggest that the animal, like *C. elizae*, pulled itself along by side-to-side movements of the stem. The sequence was probably as follows: the posterior stem was stuck obliquely into the sea-floor, somewhat to the left, by the action of the anterior stem; the stem bent still more to the left, pulling the theca backwards; the posterior stem was pulled out of the sea-floor; the stem bent slightly to right and the sequence was repeated on the right side.

Movement may not have been habitual in the adult, since most large specimens have lost the oral appendage and all the posterior stem except two or three segments.

c. ***Mitrocystella incipiens*** (Barrande) ***miloni*** Chauvel

SYSTEMATIC POSITION: Phylum: Chordata. Subphylum: Calcichordata. Class: Stylophora Gill & Caster 1960. Order: Mitrata Jaekel 1918. Family: Mitrocystitidae Jaekel 1900 (as Mitrocystidae). Genus: *Mitrocystella* Jaekel 1900. Species: *Mitrocystella* [*Anomalocystites*] *incipiens* (Barrande 1887). Subspecies: *Mitrocystella incipiens miloni* (Chauvel 1941).

OCCURRENCE: The subspecies occurs in siliceous nodules in the " Schistes à Calymènes " (Ordovician, Llandeilo Series) of Brittany. The main locality is le Grand Champ de Traveusot, Ille-et-Vilaine (Chauvel 1941 : 176). *Mitrocystella incipiens incipiens* occurs in the Šárka Beds (Llanvirn Series) of Bohemia, but is usually ill-preserved. The associated fauna of trilobites, brachiopods and molluscs indicates a shallow-water, marine environment.

MATERIAL: About 280 specimens in the Institut de Géologie, Rennes (mainly Milon Coll.); A 46271 in the Sedgwick Museum, Cambridge (MacGregor Coll.); two specimens in the Department of Geology, University of St. Andrews, Scotland (MacGregor Coll.); and seven specimens E 23664–5 and E 238885–9 in the British Museum (Natural History) (Chauvel Coll.).

Certain points of interest were seen in *Mitrocystella incipiens incipiens* from Bohemia. Three of the specimens studied are in the British Museum (Natural History) E 23606–8 and six in the Museum of Comparative Zoology, Harvard (580–5). A large number are also preserved in the Národní Museum (Prague), but of these only one, in a siliceous nodule (Acc. cat. 22011, Inv. no. 688, Šárka Beds ($d\gamma_2$), loc. Šárka, coll. Hanuš) was informative.

GENERAL SHAPE AND PLATE NOMENCLATURE: The thecal skeleton of *M. i. miloni* consists of two parts (Fig. 13a, b). There is a shield of large plates forming what is here regarded as the dorsal side (" plastron " (Caster 1952), " face inférieure "

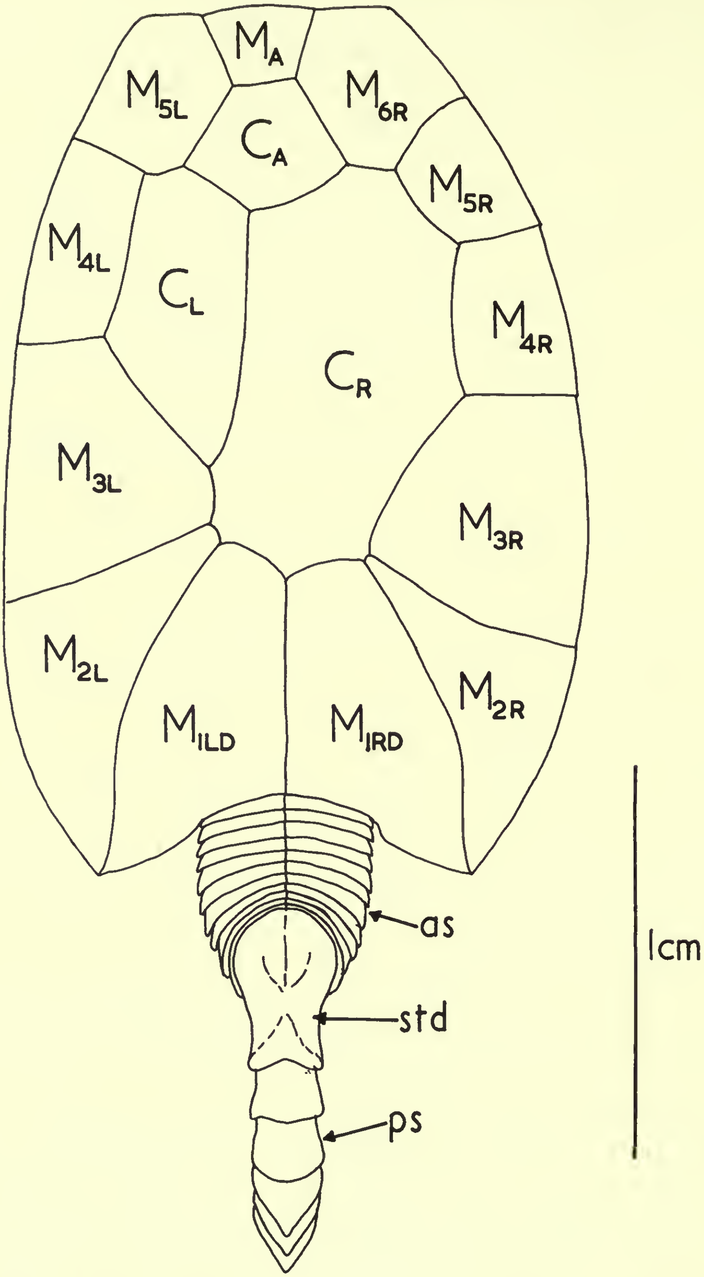

M_A
M_{5L}
C_A
M_{6R}
M_{5R}
M_{4L}
C_L
M_{4R}
C_R
M_{3L}
M_{3R}
M_{2L}
M_{1LD}
M_{1RD}
M_{2R}
as
std
ps
1cm

FIG. 13. *Mitrocystella incipiens miloni.* a. dorsal ; b. ventral ; c. right ; d. anterior ; e. posterior aspects. as = anterior stem ; bo = branchial opening ; ia = interossicular articulation ; mo = mouth ; ng = narrow groove (lateral line) ; or = oral plate ; ps = posterior stem ; std = styloid ; tr = transverse ridge ; vp = ventral plate of posterior stem ; x = point where a ventral plate imbricates over a dorsal ossicle.

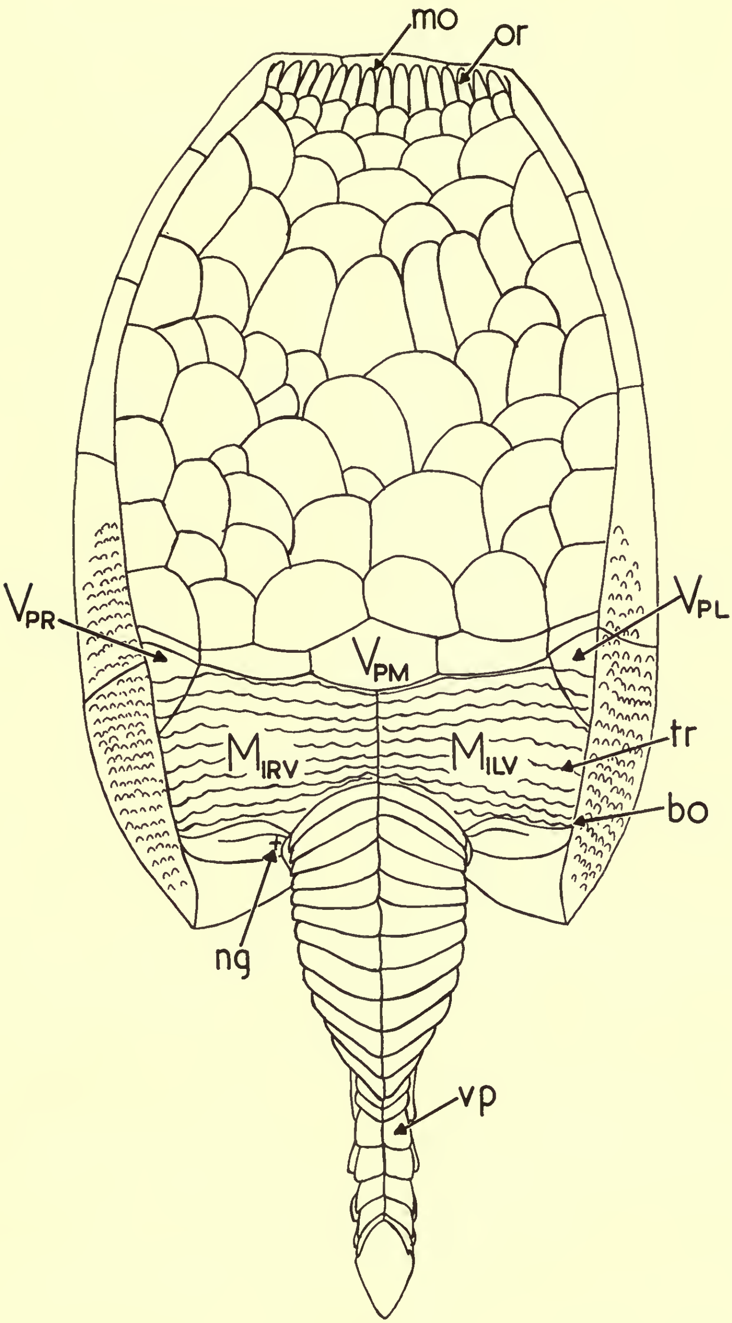

mo
or
V_{PR}
V_{PL}
V_{PM}
M_{IRV}
M_{ILV}
tr
bo
ng
vp

Fig. 13b.

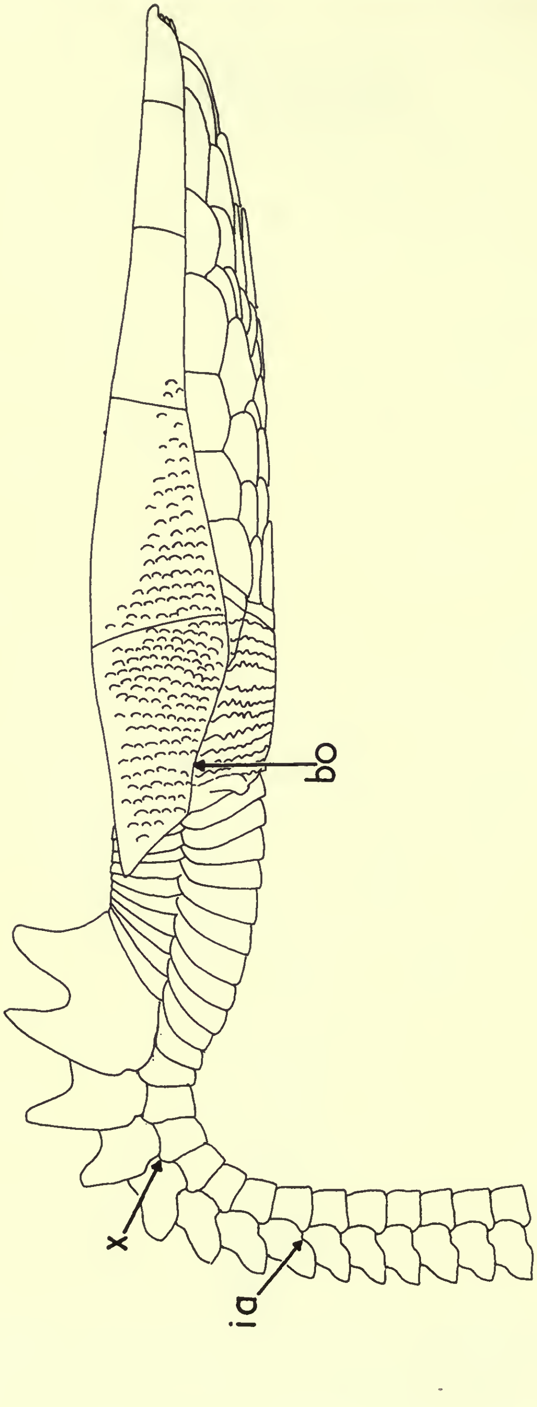


Fig. 13c.

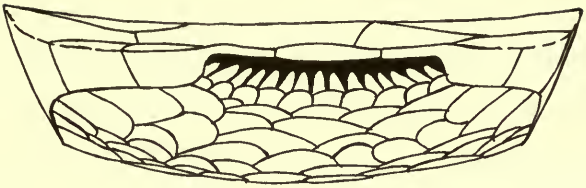


FIG. 13d.

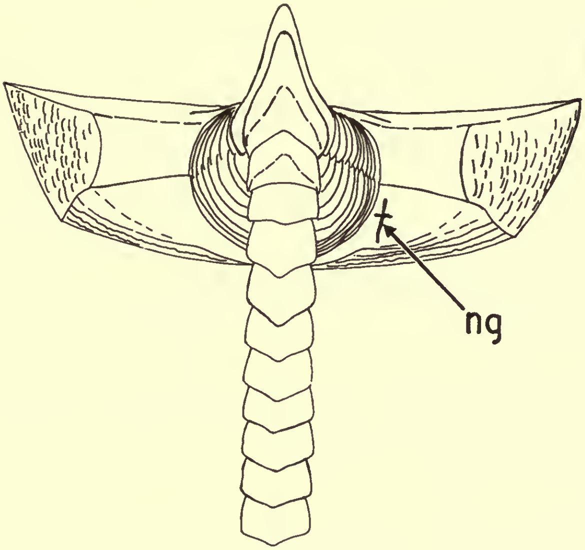


FIG. 13e.

(Chauvel 1941), " Dorsalseite " (Jaekel 1900), " Unterseite " (Jaekel 1918), " reverse side " (Gislén 1930)). The ventral face (" carapace " (Caster 1952)) was evidently more flexible except posteriorly.

The plates present in the theca are as follows:

Notation	Name	Chauvel 1941
M1LD	Left dorsal 1st marginal	M 1° marginale droite
M1LV	Left ventral 1st marginal	I + E Interbasale and épibasale
M2L	Left 2nd marginal	M_2 2° marginale droite
M3L	,, 3rd ,,	M_3 3° ,, ,,
M4L	,, 4th ,,	M_4 4° ,, ,,
M5L	,, 5th ,,	M_5 5° ,, ,,
MA	Anterior marginal	M_6 6° ,, ,,
M1RD	Right dorsal 1st marginal	M_1' 1° marginale gauche
M1RV	Right ventral 1st marginal	I + E Interbasale and épibasale
M2R	,, 2nd marginal	M_2' 2° marginale gauche
M3R	,, 3rd ,,	M_3' 3° ,, ,,

Notation	Name	Chauvel 1941
M_{4R}	,, 4th ,,	M_4' 4° ,, ,,
M_{5R}	,, 5th ,,	M_5' 5° ,, ,,
M_{6R}	,, 6th ,,	M_6' 6° ,, ,,
C_L	Left central	H_2 2° hypocentrale
C_A	Anterior central	H_3 3° ,,
C_R	Right central	H_1 1° ,,
—	Ventral plates	épicentrales
V_{PM}	Median posterior ventral	No special name
V_{PL}	Left posterior ventral	,, ,, ,,
V_{PR}	Right posterior ventral	,, ,, ,,

Chauvel's scheme, and to a lesser extent the one adopted here, is based on that of Jaekel (1918), with additions. The plates just anterior to the stem, i.e. M_{1LV}, M_{1LR}, M_{1LD} and M_{1RD}, must be homologous with the like-named plates in cornutes. The homologies of the other plates are unclear, except that the marginals must be broadly homologous with those of cornutes.

The stem is divided into anterior, medial and posterior parts as in the cornutes. Details of the stem skeleton are given below (p. 289).

Thecal openings: The mouth (mo in Fig. 13b) faces slightly leftwards (cf. p. 314). It is bordered above by part of the rigid dorsal shield (M_{6R}, M_A, M_{6L}) and below by about fifteen elongate oral plates (or). These are fixed to a flexible lower lip, studded with post-oral plates, which is dorsal to the front edge of the ventral armour.

The rigid skeleton above the mouth of *M. i. miloni* contrasts with the situation in *Cothurnocystis elizae* where the skeleton was rigid beneath the mouth. An intermediate situation exists in the earliest known mitrocystitid (*Chinianocarpos thorali* Ubaghs from the Upper Tremadoc or Lower Arenig Series of the Montagne Noire), where the mouth is entirely surrounded by large plates, i.e. M_A dorsally, M_{5R} and M_{5L} ventrally (Ubaghs 1961*a* and personal observation).

There are no external branchial slits in *M. i. miloni.* Paired, external, branchial openings (bo in Figs. 13b, c, 15H) seem to have existed, however, near the posterior right- and left-hand corners of the theca. The roughly horizontal suture between M_{1D} and M_{1V} on each side is curved (Fig. 15I) as if to facilitate articulation (cf. Fig. 7) about the length of the suture. When M_{1V}, because of high pressure inside the theca, rocked backwards on this suture, an opening would appear between it and M_2, and close again when M_{1V} rocked forwards as the pressure fell. The opening would thus behave as an outlet valve. It would be faced on both sides almost entirely by the connective tissue of the middle layer of the skeleton (Fig. 15H) which would provide a seal like that round the branchial slits of *C. curvata.* The nerve n_3 (optic) ran just anterior to the opening while n_4 ran just median to it. The branchial openings rested on the substratum but the analogy of modern rays and skates shows that they could have functioned in this position. *M. mitra* (p. 314) had similar branchial openings which are in some ways easier to interpret.

There was no external anus in *M. i. miloni*, as discussed below (p. 287).

A narrow vertical groove on $\mathrm{M}_{1\mathrm{RV}}$ (ng in Fig. 13b, c; Pl. 4, fig. 9) is here regarded as a rudimentary lateral line (cf. p. 307, below). It sometimes has a short horizontal groove across it (Pl. 9, fig. 4).

THE CHAMBERS OF THE THECA: A direct picture of the chambers of the theca (Fig. 14a, b) can be obtained from the internal cast, whose surface is traversed by grooves which separate the original chambers and correspond to ridges on the skeleton.

A groove (oblique groove), running from near the right side of the mouth to near the left side of the stem, is the most notable feature of the dorsal side of the internal cast. This groove (" sillon transversal " of Chauvel 1941) is not symmetrical in section. For most of its length it is steeper to the right than to the left so that it grossly separates a left, anterior, ventral chamber from a right, posterior, dorsal chamber.

The oblique groove is here held to be broadly homologous with the pharyngo-visceral line of *Cothurnocystis elizae*. The chamber anterior and to the left of it corresponds to the pharynx of *C. elizae* and is henceforth called the left pharyngeal chamber. The chamber posterior to, and to the right of, the oblique groove is broadly homologous with the anterior coelom of *C. elizae*, apart from some complexities which are discussed below.

The oblique groove is flexuous and varies in strength. Anteriorly it bays out to the right. For a short distance in the anterior part of this embayment the left side of the groove is steeper than the right side (Fig. 15 A; Pl.5, figs. 7, 9). Here, therefore, the left pharyngeal chamber overlay the anterior coelom. In the middle of the embayment the groove is shallow and symmetrical (Fig. 15B; Pl. 5, figs. 1, 7, 9). In the posterior part of the embayment it deepens, has a rounded floor, and is steeper to right than to left (Fig. 15C). Behind the embayment the groove sends out a median branch (mb in Pl. 9, fig. 2). This is triangular in section (Fig. 15D), tapers posteriorly, and is largely hidden in the internal cast. For a short distance behind and left of the separation of this median branch the oblique groove again has a rounded floor and is symmetrical (Fig. 15D; Pl. 9, fig. 2) or has the right side only a little steeper than the left. Behind this the floor of the groove suddenly becomes angular (at point v in Pl. 9, fig. 2), with the right side distinctly steeper than the left (Fig. 15E). The depth, angularity and asymmetry of the groove increase gradually backwards (Fig. 15F). Posteriorly the oblique groove gives rise to two other grooves. The left one of these runs backwards and then vertically downwards while the other (" sillon pedonculaire " of Chauvel 1941) turns to the right.

The anterior embayment and weakening of the oblique groove suggest an outpouching from the left pharyngeal chamber. This outpouching is henceforth called the right pharyngeal chamber; in ontogeny it must have pushed the anterior coelom upwards and partly obliterated its lumen.

The median boundary of the right pharyngeal chamber is indicated anteriorly by the median branch of the oblique groove and more posteriorly by a very weak

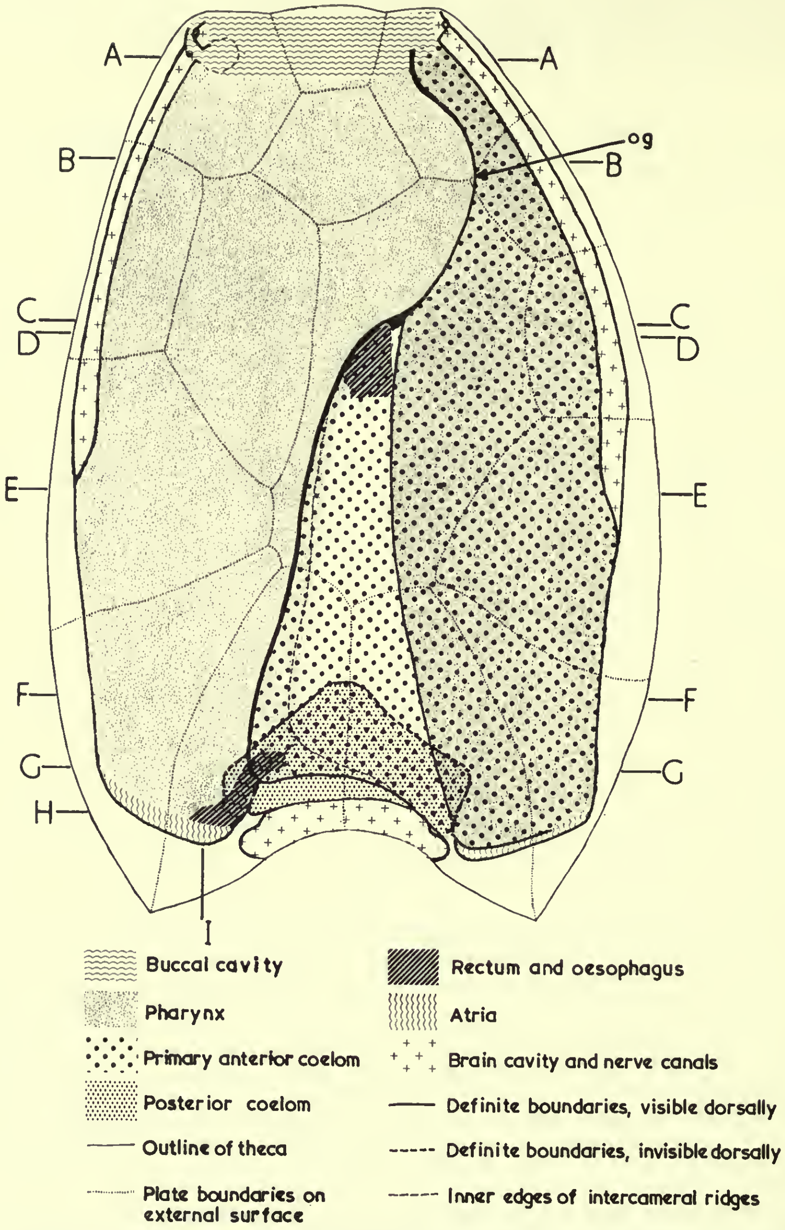

A
A
og
B
B
C
D
C
D
E
E
F
F
G
G
H
I
Buccal cavity
Rectum and oesophagus
Pharynx
Atria
Primary anterior coelom
Brain cavity and nerve canals
Posterior coelom
Definite boundaries, visible dorsally
Outline of theca
Definite boundaries, invisible dorsally
Plate boundaries on external surface
Inner edges of intercameral ridges

FIG. 14. *M. i. miloni.* Chambers of theca. a. dorsal ; b. posterior aspects. og = oblique groove. A—A to G—G, H and I indicate planes of section used in Text-fig. 15. Stipple is used here as in Text-figs. 4 and 10.

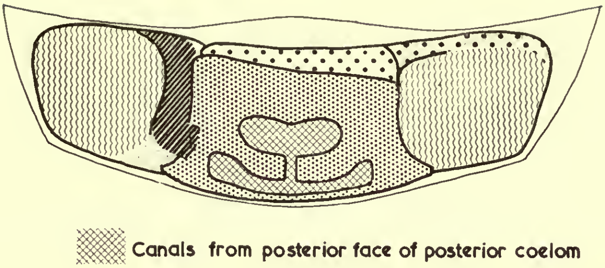


Fig. 14b.

groove (grp in Pl. 5, fig. 1 and Pl. 10, fig. 1) running from the right side of the median branch to a point just right of the stem. This groove is weak because it does not correspond to any actual gap between chambers at the surface of the skeleton (cf. Fig. 15E, F).

In ontogeny the left pharyngeal chamber evidently preceded the right pharyngeal chamber, and it is therefore likely that the left gill slits preceded the right ones. This is what happens in the ontogeny of amphioxus (Willey, 1894, p. 130 ff.).

The rounding of the floor of the oblique groove just behind and left of the median branch may indicate that the oesophagus opened here into the left pharyngeal chamber. There are two reasons for this supposition. Firstly, the exact form of the internal cast (Pl. 9, fig. 2) suggests that some roughly cylindrical structure was in contact with the skeleton here. Secondly, by analogy with tunicates, the oesophagus should open into the pharynx in a median, dorsal position. Comparison with tunicates is reasonable on account of the disposition of the rectum, as discussed below.

The posterior coelom (pco) is delimited by the above-mentioned, right and left posterior grooves arising from the oblique groove. These sweep round the posterior coelom and meet ventrally.

The right posterior groove corresponds dorsally to Chauvel's " sillon pedonculaire ". The dissection shown on Pl. 5, fig. 10, shows the oblique ridge (obr, i.e. the skeletal filling of the oblique groove) curving round gradually into the ridge filling this " sillon pedonculaire " (rpco). The exposed surface of the oblique ridge in this dissection consists of skeleton deposited against the limiting membrane of the left pharyngeal chamber. The exposed surface of the ridge (rpco) consists of skeleton deposited against the limiting membrane of the posterior coelom. The smooth connection between these two ridges in the dissection suggests that these membranes were, in fact, one and the same. The same dissection also suggests that the leftward limit of the posterior coelom (llpc), i.e. the left posterior groove arising from the oblique groove, was a fold in this membrane increasing in sharpness posteriorly. It follows that the posterior coelom became constricted off during ontogeny from the left pharynx when left pharynx and anterior coelom were already separate entities. This mode of origin of the posterior coelom is reminiscent of the origin of an epicardium in a tunicate, and it is noteworthy that Berrill (1955 : 101) regarded epicardia as homologous with coeloms. The groove on the internal cast to the left of the posterior ceolom is almost interrupted, towards its ventral end, by a bridge (rb in Pl. 5, fig. 4) whose significance is discussed below.

Two further chambers (Fig. 14a, b; ra in Pl. 9, fig. 1), situated right and left of the posterior coelom, must represent atria, for they lie between the gill openings and the presumed positions of the internal gill slits. The atria are distinctly unsymmetrical and the right one touches the posterior coelom along its whole median border. The left one, on the other hand, does not touch the posterior coelom, from which it is separated by a vertical hemicylindrical ridge (rr in Pl. 5, fig. 4) on the internal mould. This ridge connects ventrally with the bridge (rb) across

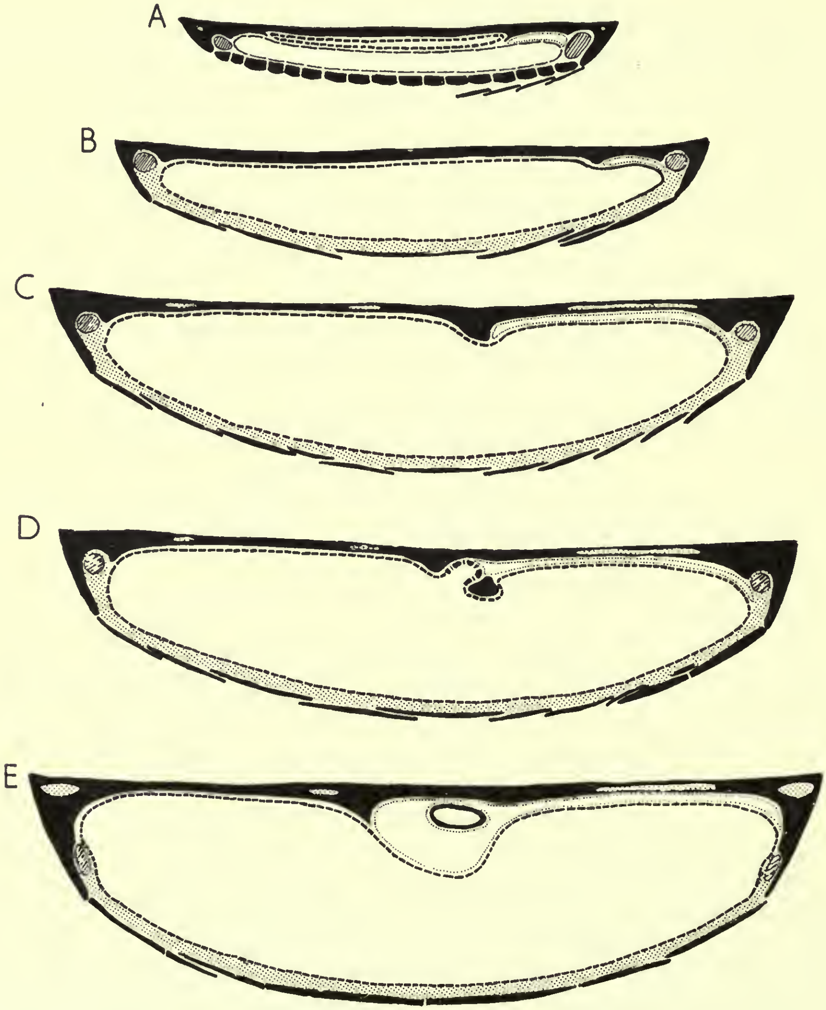


Fig. 15. *M. i. miloni.* Sections through theca to show disposition of membranes limiting chambers, and other features of the soft anatomy. bo = branchial opening.

the groove to the left of the posterior coelom. Both atria are delimited dorsally in some specimens by weak, horizontal grooves on the internal mould.

By analogy with *Cothurnocystis elizae* and *C. curvata* the rectum probably left the posterior coelom near the ventral, left posterior corner of the latter, i.e. by the bridge rb. Again by analogy with *C. elizae* and *C. curvata*, the rectum then ran vertically upwards, i.e. along the ridge rr, and must then have opened into the left atrium. Faeces would be washed away by the current through the left gill slits almost exactly as in *C. elizae* and *C. curvata*, and would finally leave the theca through the left gill opening.

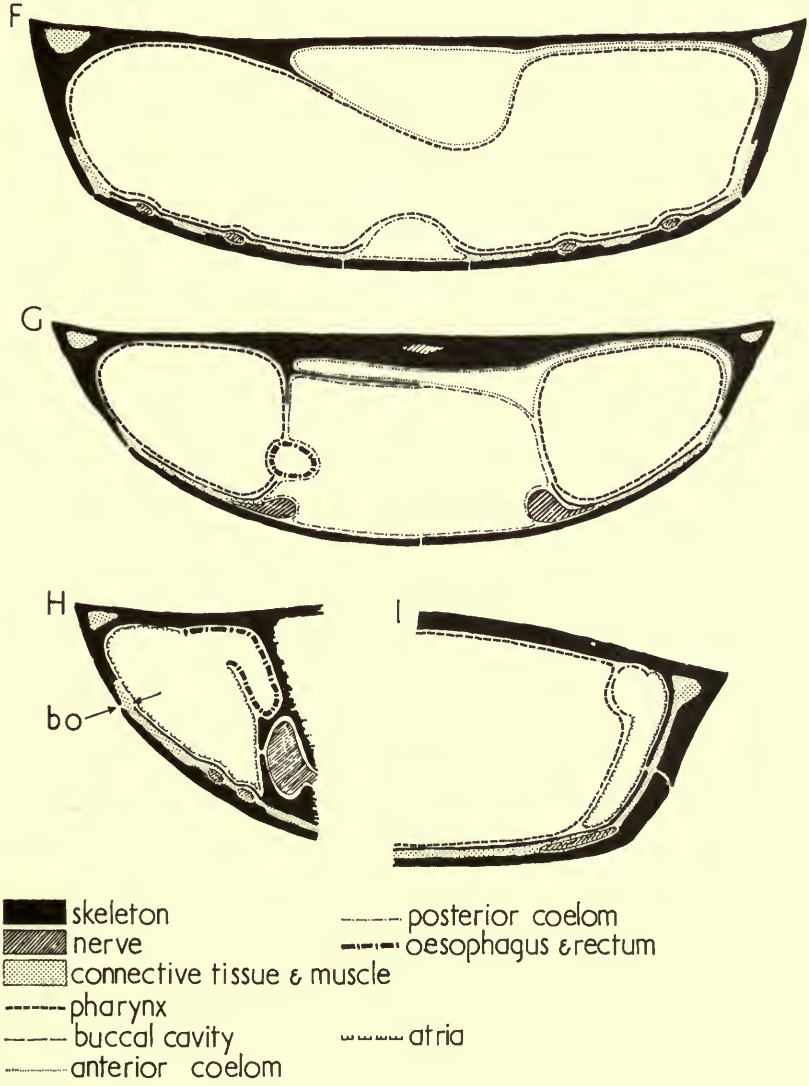

F
G
H
bo
I
skeleton
nerve
connective tissue & muscle
pharynx
buccal cavity
anterior coelom
posterior coelom
oesophagus & rectum
atria

FIG. 15, F–I.

In a similar way the rectum of a tunicate tadpole either opens into the left atrium, or its closed end touches the left atrium, to open there after metamorphosis (Fig. 16; Julin 1904; Grave 1921, 1944; Kowalevsky 1867, 1871; Garstang 1928).

The existence of a buccal cavity shows clearly on the internal moulds of several specimens (bc, Pl. 5, fig. 7) just left of the mouth, where it evidently touched the dorsal skeleton (M_{5L}). Its wall was lightly calcified near the contact with the dorsal skeleton and can be followed by dissection a short way into the internal cast (Pl. 5, fig. 9). No similar structure can be found right of the mouth where the buccal cavity was probably separated from the skeleton by the pharynx and anterior coelom (Fig. 15A). The broad shape of the internal mould is the same, however, suggesting that the buccal cavity affected the dorsal skeleton without actually touching it. The relationship of the oblique groove with the buccal cavity of *M. i. miloni* is almost exactly like that of the pharyngo-visceral line and buccal cavity of *C. elizae*.

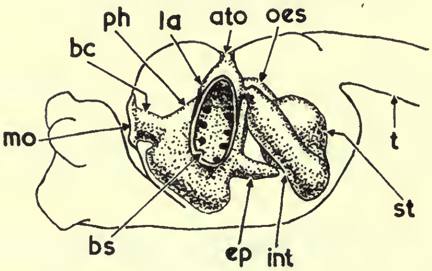


Fig. 16. Alimentary canal of the tadpole larva of the tunicate *Clavelina rissoana*, left aspect, redrawn after Julin (1904, fig. 12). ato = atrial opening ; bc = buccal cavity ; bs = branchial slit ; ep = epicardium ; int = intestine ; la = left atrium ; mo = mouth ; oes = oesophagus ; ph = pharynx ; st = stomach ; t = tail.

The thecal chambers of *M. i. miloni* and *Cothurnocystis elizae* were, therefore, basically the same. The most fundamental difference is the appearance in *M. i. miloni* of the right pharyngeal chamber, which pouched out from the primary or left pharyngeal chamber towards the posterior, right-hand corner of the theca. In so doing, the right pharyngeal chamber lifted the anterior coelom off the floor of the theca and partly obliterated its lumen. For this reason, the junction between anterior coelom and the left or primary pharyngeal chamber (oblique groove of mitrates; pharyngo-visceral line of cornutes), which runs in both cornutes and mitrates from right of the buccal cavity to left of the stem, is in mitrates fixed to the ceiling of the theca, instead of to the right, posterior side wall. Indeed, for much of its length in *M. i. miloni* it traverses a central plate, i.e. its course is across M_{1LD}, C_R, M_{5R} and M_{6R}. It is interesting to note, therefore, that in the earliest known mitrocystitid, *Chinianocarpos thorali*, the oblique groove likewise runs across the ceiling of the theca, much as in *M. i. miloni* (Ubaghs 1961*a*, and personal observation). In addition, variations in its depth and direction in *C. thorali* indicate that the right pharyngeal chamber already existed. On the other hand, as in *C. elizae*, the roof of the left pharyngeal chamber is a flexible integument and the oblique groove is entirely borne on marginal plates (M_{1LD} and M_{4R}). It is as if, in phylogeny, the oblique groove of *C. thorali* had been carried forwards and leftwards by dorsal extensions of the posterior right-hand marginals.

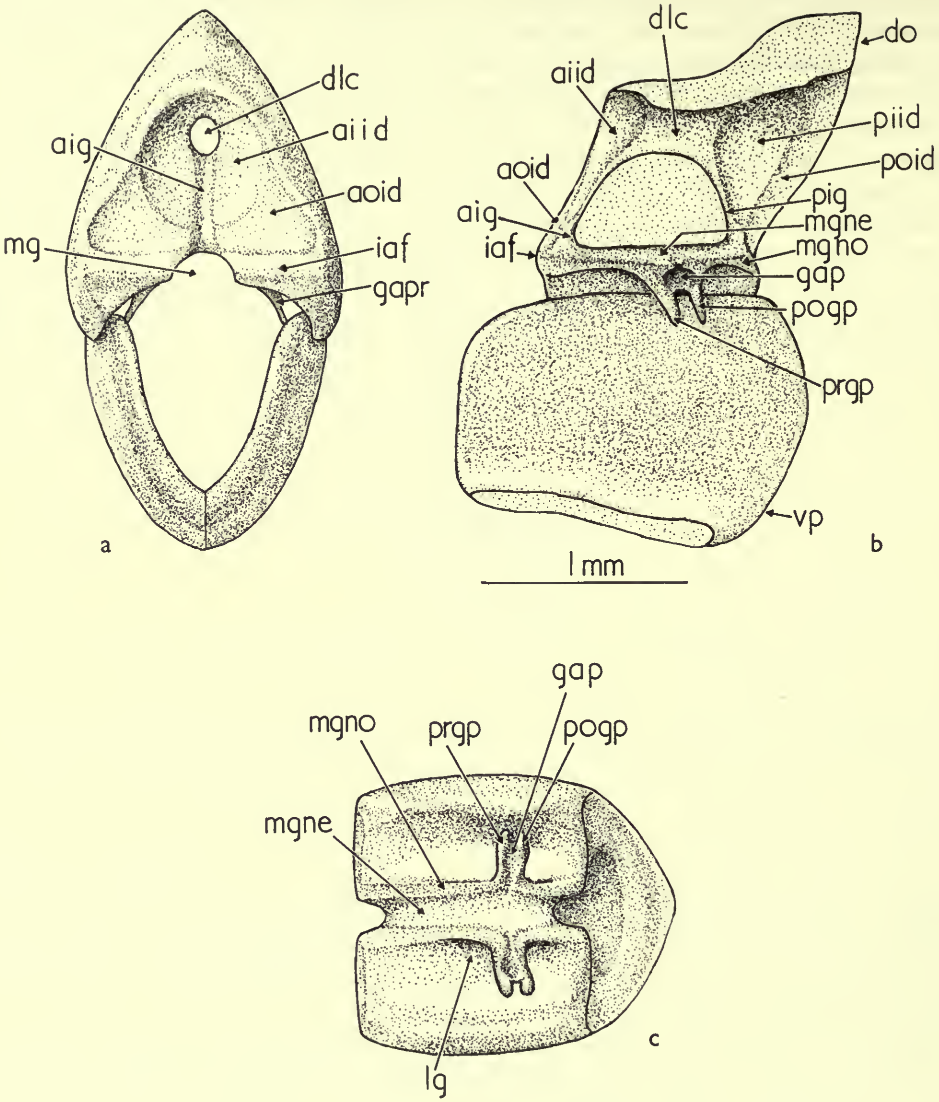
The basically similar disposition of the chambers of the theca in mitrates and cornutes strongly indicates, contrary to most previous authors, that the big-plated side of mitrates corresponds to the dorsal side of cornutes and was uppermost in life.

Two objections to this orientation need to be dealt with. Firstly, in the earliest known lagynocystid mitrate, *Peltocystis cornuta* Thoral from the Upper Tremadoc or Lower Arenig Series of the Montagne Noire, the oblique groove sometimes runs from anterior left to posterior right. This is a most abnormal occurrence among mitrates, however, and is unknown in Mitrocystitidae and so can be disregarded. Secondly, if the strut of cornutes were homologous with the ridge filling the oblique groove of mitrates, orientation with the big-plated side downwards would be implied. Such a homology is most unlikely. The strut does not resemble an intercameral ridge, and was probably a purely mechanical feature (p. 258) that lost its function and disappeared when one face of the animal came to be built of big plates. If the strut were homologous with the oblique ridge there would be no homologue in mitrates for the pharyngo-visceral line.

In summary, therefore, the chambers of the theca of *M. i. miloni* consisted of buccal cavity, left pharyngeal chamber, right pharyngeal chamber, anterior coelom, posterior coelom and left and right atria. In ontogeny the left pharyngeal chamber must have been separate from the anterior coelom from a very early stage. The right pharyngeal chamber certainly, and the posterior coelom probably, arose as outpouchings from the left pharyngeal chamber. The rectum opened into the left atrium as in a tunicate tadpole. Left gill slits probably preceded right gill slits in ontogeny as in amphioxus. In its probable origin from the pharynx, the posterior coelom can be compared with a tunicate epicardium. The oesophagus probably opened into the left pharyngeal chamber near the junction with the right pharyngeal chamber. It was the big-plated side of *M. i. miloni* that was uppermost and corresponded to the dorsal side of a cornute. Finally, the earliest-known mitrocystitid was in some ways transitional, in the arrangement of its chambers as in other respects, between cornute and mitrate conditions.

THE STEM: The posterior stem of *M. i. miloni* consists of about fifteen segments and ends abruptly. Each segment contains a dorsal ossicle (do in Fig. 17b) and paired ventral plates (vp). Successive dorsal ossicles articulate with each other at inter-ossicular articulations (iaf in Fig. 17b) which would have allowed vertical flexing.

The precise mode of imbrication of plates and ossicles is important (Fig. 18). Dorsal to the interossicular articulation the back of each ossicle overlaps the front of the one behind. Similarly, the back of each pair of ventral plates overlaps the front of the pair behind. The lateral, ventral margins of a dorsal ossicle overlap the upper margins of the ventral plates of the same segment. But, certainly in *M. barrandei* (at x in Pl. 6, figs. 3, 5) and probably in *M. i. miloni* in the uncrushed condition (Pl. 5, fig. 5 at point x), the posterior, upper corners of a ventral pair


dlc
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a
dlc
do
aiid
piid
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mgne
iaf
mgno
gap
pogp
prgp
vp
b
1 mm
gap
mgno
prgp
pogp
mgne
c
lg

Fig. 17. *M. i. miloni.* Reconstruction of the skeleton of a posterior stem segment. a. anterior aspect; b. sagittal section; c. ventral; d. posterior aspect. aig = anterior ossicular groove ; aiid = anterior inner, interossicular depression ; dlc = dorsal longitudinal canal ; do = dorsal ossicle ; gap = ganglionic pit ; gapr = ganglionic process ; iaf = interossicular articular facet ; mg = median groove ; mgne = median groove (neural) ; mgno = median groove (notochordal) ; pig = posterior interossicular groove ; piid = posterior inner interossicular depression ; pagp = postganglionic process ; poid = posterior outer interossicular depression ; prgp = preganglionic process ; vp = ventral plate.

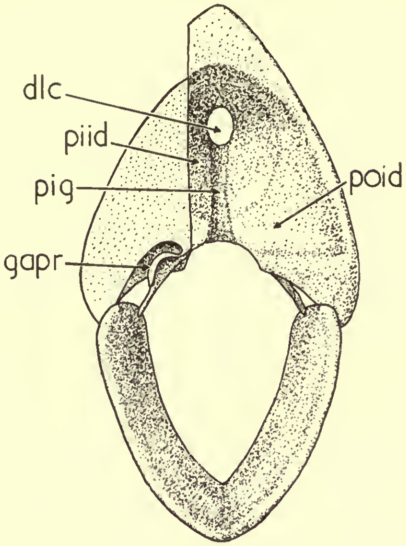

Fig. 17d.

of plates embrace the lower front corners of the next dorsal ossicle behind. A similar imbrication pattern, but with the ventral plates overlapping the dorsal ossicle behind still more extensively, also exists in *Chinianocarpos thorali* (Ubaghs 1961*a*, fig. 1E, and personal observation).

According to Prof. Ubaghs' interpretation (1961*b*) the ventral stem plates of mitrates, which he homologizes with the dorsal stem plates of cornutes, were cover plates capable of opening outwards, and the whole stem was an arm. It is clear that the imbrication just described is very ill-suited to allow the ventral plates to open outwards and, like the detailed stem structure of *Cothurnocystis curvata* (p. 276), argues against Prof. Ubaghs' interpretation. It is also clear that Prof. Ubaghs must be mistaken if, as here maintained, the massive posterior stem ossicles were dorsal in mitrates and ventral in cornutes, for in neither case can the sculpture on their internal surfaces correspond to the *outside* of a water-vascular system.

The internal sculpture of the posterior stem ossicles is very complicated (Fig. 17, 18; Pl. 6, figs. 10, 11; Pl. 7, fig. 5). Above the articulations each ossicle is excavate at back and front, with posterior and anterior, inner and outer depressions (aiid, aoid, piid, poid). Also, in the median plane, there are anterior and posterior inter-ossicular grooves (aig and pig) which connect with a dorsal, longitudinal canal (dlc) perforating the ossicle. On the ventral surface of the more anterior ossicles there is a broad, median groove (mg) which becomes progressively deeper posteriorly in the stem till it passes, in the most posterior ossicles, into a median canal (mc in Pl. 6, fig. 5). In each ossicle the median groove or canal gives rise to paired pits (gap). Each pit is excavated in the ventral surface of a process (gapr) which bifurcates outwards into two prongs (prgp anteriorly and pogp posteriorly). On each side of the median groove, in the ventral surface of the ossicle, are lateral grooves (lg). Sometimes the lateral grooves are deepest over the processes gapr (Fig. 17c; Pl. 6, fig. 5). Sometimes, on the other hand, the lateral grooves are filled with skeleton dorsal to those processes, in which case the natural moulds of the pits on gapr are visible dorsally (Pl. 6, fig. 10; Pl. 7, fig. 4).

The structure of the median groove or canal is highly significant. The groove or canal seems to have enclosed two longitudinal soft structures. The first of these was broadly cylindrical and determined the fundamental shape of the groove or canal. It came in actual contact with the parts of the groove marked mgno in Fig. 17b, c. The second structure was thin and strap-like and coated part of the dorsal surface of the first structure. It occupied the parts of the groove marked mgne in Fig. 17b, c and sent out lateral projections to the cups of the processes gap. Natural moulds of the median groove, giving a representation in rock of the original soft structures, are shown in Pl. 6, fig. 10 and Pl. 7, fig. 2. The more dorsal structure became narrower, thinner and less evident posteriorly.

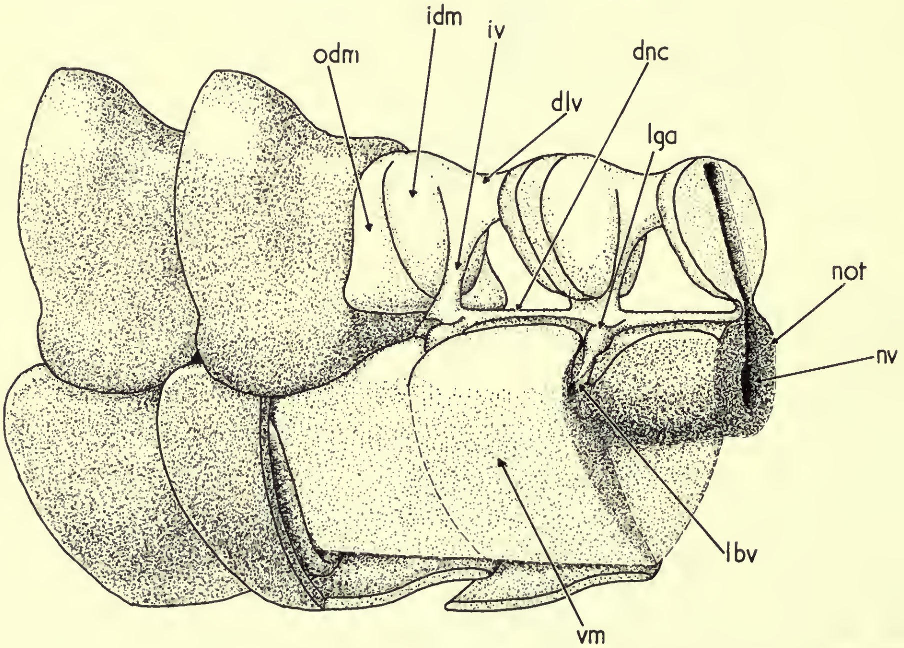

FIG. 18. *M. i. miloni.* Block diagram of posterior stem. dlv = dorsal longitudinal vessel; dnc = dorsal nerve cord; idm = inner dorsal muscle; iv = interossicular vessel; lbv = lateral blood vessel; lga = lateral ganglion; not = notochord; nv = notochordal vessel; odm = outer dorsal muscle; vm = ventral muscle.

As regards interpretation, the broad cylindrical structure in the median groove, by analogy with crinoids, was the chambered organ. Being an anti-compressional structure it was placed at the level of the interossicular articulations, in the principal axis of the stem, which would not shorten or lengthen on bending. Again by analogy with crinoids, the structure coating the chambered organ would be the peduncular nerve. Its nervous nature is consistent with its strap-like shape and with the way it communicates with the cups of the processes gap (ganglionar processes), for such cups could well contain ganglia. The peduncular nerve of *M. i. miloni* therefore rested on the dorsal surface of the chambered organ, or, in chordate terms, the dorsal nerve cord rested on the dorsal surface of the notochord. It is noteworthy that the dorsal nerve cord rests directly on the notochord in tunicate tadpoles, amphioxus, Agnatha and the embryos of other vertebrates, and also in myxinoids and petromyzontoids it has, as in *M. i. miloni*, a distinctly strap-like shape. The paired segmental ganglia of *M. i. miloni* can be compared with those in the tail of appendicularians (Martini 1909). There is no trace of separate dorsal and ventral spinal nerve roots. The nervous and other soft structures of the posterior stem of *M. i. miloni* are reconstructed in Fig. 18.

Turning now to the musculature, the posterior stem could either flex ventrally or stick out straight, as indicated by the interossicular articulations and imbricating ventral plates. This is confirmed by fossils evidently preserved in the position of death. Pl. 6, figs. 3, 6 (*M. barrandei*); Pl. 7, fig. 5 (*M. incipiens incipiens*) and Pl. 5, fig. 5 (*M. i. miloni*) show straight posterior stems or portions of them. Conversely, Pl. 10, fig. 2 (*M. i. miloni*) shows the stem bent ventrally in the normal position of preservation for the subspecies. Muscles would therefore be needed on at least one side of the articulations, i.e. either dorsally or ventrally, and muscles or ligaments on the other side.

It seems likely that the space between dorsal ossicles and ventral plates was largely filled with muscle. The opposing muscles or ligaments must have been sited in the interossicular depressions. The inner interossicular depressions are very deep and therefore probably contained muscle. The outer interossicular depressions may have contained ligament, or a different sort of muscle. The structure (probably a blood vessel) filling the interossicular grooves probably separated right and left muscle blocks in the interossicular depressions. Repetition of interossicular depressions indicates serial repetition of dorsal muscle blocks.

The ventral muscles were probably also segmented, with the muscle blocks situated between the ganglia. The divisions between muscle blocks are indicated by: 1. the above-mentioned skeletal infilling that sometimes interrupts the lateral grooves dorsal to the ganglionar processes; and 2. the occasional presence of faint ridges on the ventral surface of the ossicle, or grooves in the internal mould, which point downwards and backwards (gmb in Pl. 7, fig. 5) and whose upper ends coincide in position with the ganglia.

The blood system of the posterior stem is difficult to reconstruct. It probably included: 1. a dorsal longitudinal vessel (dlv), occupying the dorsal longitudinal canal; 2. interossicular vessels (iv in Fig. 18), occupying anterior and posterior interossicular grooves; 3. transverse vessels, connected with the sides of the notochord (lbv in Pl. 9, fig. 3) ventral to the segmental ganglia; and 4. a notochordal vessel running down the middle of the notochord.

The evidence that the interossicular grooves carried blood vessels is that: 1. although they emerge from the notochord through the dorsal nerve cord, they seem to be too wide to have carried only an upward extension of the nerve cord, so far as the thickness of the nerve cord can be judged from the form of the median groove; 2. the dorsal muscles would need a blood supply. In the mitrate *Lagynocystis pyramidalis* interossicular depressions for dorsal muscle and interossicular grooves were present (personal observation) but there was no dorsal longitudinal canal. In this form, therefore, the dorsal muscles must have been supplied with blood up the interossicular grooves. By analogy it is therefore likely that the interossicular grooves of *M. i. miloni* also carried a blood vessel.

The existence of a vessel down the middle of the notochord is not certain, but is suggested by the following pieces of evidence: 1. The crinoids have such a vessel (haemal strand); 2. The interossicular and transverse vessels, which are joined to the notochord, could well have connected with a notochordal vessel. At the least, they indicate extensive vascularization inside the notochord; 3. There was probably no longitudinal vessel ventral to the notochord in *M. i. miloni* since none could have existed in cornutes, and no vessels which could have come directly from a ventral longitudinal vessel are seen to connect with the ventral side of the notochord when this is enclosed by skeleton (Pl. 9, fig. 3); 4. *L. pyramidalis* lacked a dorsal longitudinal vessel. Assuming, for the reasons given under (3), that this form also lacked a ventral longitudinal vessel, then a notochordal vessel must have existed. In such a fundamental feature *M. i. miloni* would probably resemble *L. pyramidalis*.

In summary, the posterior stem of *M. i. miloni* certainly had a notochord, a dorsal nerve cord giving rise to paired, segmental ganglia, and segmentally repeated muscle blocks. The vascular system included a dorsal longitudinal vessel, interossicular vessels that left the notochord through the dorsal nerve cord, transverse vessels, and probably a longitudinal vessel inside the notochord. The dorsal nerve cord resting directly on the notochord is a prime chordate feature. The vascular system, so far as can be worked out, seems to have been more like that of a crinoid.

The medial stem of *M. i. miloni* much resembles two posterior stem segments (std in Fig. 13a) with the dorsal ossicles fused to form what is known as a styloid (Jaekel 1918). The posterior surface of the styloid is very much like that of a normal dorsal ossicle (Pl. 7, fig. 3) with inner and outer, posterior interossicular depressions (piid, poid), interossicular articulations and posterior, interossicular groove (pig). The most obvious difference from a normal dorsal ossicle is that the dorsal longitudinal canal turns sharply upwards anteriorly. The interossicular grooves between the two segments of the styloid fuse to form an interossicular canal (ic) which presumably ran upwards to join the dorsal longitudinal canal. Neither the middle part of the dorsal longitudinal canal of the styloid, nor the dorsal part of the interossicular canal have been seen, however. The anterior surface of the styloid carries a broad lumen (als in Pl. 6, fig. 12), presumably serially homologous with anterior inner and outer interossicular depressions of a posterior stem ossicle. The dorsal longitudinal canal entered this lumen dorsally. A vertical groove (vgls of Pl. 6, fig. 12) posteriorly must be serially homologous with the anterior, interossicular grooves. The lateral grooves (lg) of the styloid produce a serrated internal mould with the deepest parts of the groove dorsal to the segmented ganglia. The median groove differs little from that of the posterior stem ossicles.

The anterior stem is usually poorly preserved but probably contains about ten segments. The skeleton of each segment consists of four plates (left, dorsal and ventral, and right, dorsal and ventral) round a broad lumen. In *M. barrandei* (Pl. 6, figs. 3, 5) the anterior stem could certainly flex upwards so as to lift the posterior stem; this was presumably also possible in *M. i. miloni*. By analogy with *Mitrocystites mitra* (p. 322) the anterior stem of *M. i. miloni* could probably also flex sideways. In order to flex without telescoping, a median, anti-compressional structure would be needed, i.e. a chambered organ or notochord. There must also have been muscles, probably divided into segmental blocks, a dorsal nerve cord, segmental nerves and a longitudinal blood vessel or vessels.

The reason why the massive ossicles of the posterior stem of mitrates were dorsal, whereas those of cornutes were ventral, is almost certainly functional. The posterior stem of cornutes was adapted for flexing upwards and the necessary shortening of the dorsal side was made possible by a series of imbricating plates. The posterior stem of mitrates was adapted for flexing downwards and the imbricating plates are therefore ventral, while the articulations between the massive dorsal ossicles prevented shortening along the principal axis.

Chinianocarpos thorali, as in other features, is transitional in the posterior stem structure from the cornute condition. Like all other mitrates it has an imbricating series of plates ventrally and a series of articulated ossicles dorsally, so that the stem must have been able to flex downwards. However, the ossicles are relatively less massive than in *M. i. miloni* and *Mitrocystites mitra*, and the ventral plates relatively larger. Also, in the only two specimens of *C. thorali* where the posterior stem is known (personal observation and Ubaghs 1961*a*, Fig. 1D, E) the posterior stem definitely curves gently upwards.

The actual transition between cornutes and mitrates must have had neither styloid nor stylocone, but simply two segments like those of the posterior stem, articulated with each other so that they could bend either up or down. The redevelopment of a solid element in the medial stem, preventing the anterior stem muscles from pulling against the posterior ones, would be highly advantageous.

THE BRAIN AND CRANIAL NERVES: The brain and cranial nerves of *M. i. miloni* can be reconstructed in detail (Fig. 19a, b, c) partly because they were extensively enclosed by skeleton, and partly because, when nerves ran in soft-tissue-filled spaces in the skeleton, their exact positions can often be determined. Thus, in the posterior ventral skeleton, the nerves ran in an extensive, median, soft layer (Fig. 15F, G, H, I), presumably consisting of connective tissue, between a thin inner and a thick outer layer of calcite. The positions of the nerves are indicated by dilatations of the soft layer. These dilatations are flanked by flat-topped thickenings of the outer layer (tol in Pl. 5, fig. 8), and often roofed over by gentle folds in the inner layer (as in Pl. 5, fig. 11). The inner layer of calcite is absent from the median and anterior, more flexible parts of the ventral skeleton, and the connective tissue layer, if it existed in this region, cannot be recognized.

Upward extensions from the median layer of the ventral skeleton entered the dorsal skeleton near the posterior right and left corners of the theca (Fig. 15I) and there remained separate from the thecal cavity because of an inner layer of calcite. More anteriorly and laterally other extensions from the median soft layer of the ventral skeleton touched the inner face of the dorsal skeleton which was excavated to receive them (Fig. 15F, G, H; sl in Pl. 7, fig. 6), but these extensions were not separated from the thecal cavity by an inner layer of calcite.

In addition to these direct upward extensions of the ventral median layer, the dorsal skeleton contained an extensive irregular system of spaces in the calcite. These spaces must have been filled with soft tissue and are particularly evident across sutures (e.g. sl in Pl. 6, fig. 7).

The histological origin of the soft-tissue-filled spaces could not be studied, in the absence of material showing actual stereom mesh. Resorption of calcite may have played a part in their origin, but of this there is no proof. The presence of casts of a calcite cleavage network (ccc in Pl. 5, fig. 2; Pl. 6, fig. 7) is the only direct indication that the hard skeleton was calcite.

The nervous nature of the structures here called nerves, which was already recognised by their discoverer Chauvel (1941), is virtually certain because: 1. like the aboral nerves of crinoids they radiate from the region where the stem joins the theca; and 2. they often had a very compressed cross section (Fig. 15F, G; Pl. 5, figs. 6, 8, 11).

The brain, as in cornutes, was lodged in the theca, just in front of the stem. The encephalic mould is divided into anterior (ap), medial (mp) and posterior (pp) parts (Fig. 19a–c; Pl. 6, figs. 1, 4). The anterior part is frond-shaped and developed along the posterior, median, dorsal suture (M_{1LD}/M_{1RD}). The medial and posterior parts, like the brain of cornutes, lie in a cerebral depression which, however, is excavated in the dorsal instead of the ventral first marginals, i.e. M_{1L} and ${}_{RD}$ instead of M_{1L} and ${}_{RV}$. The side walls of the posterior part of the cerebral depression received the most anterior plates of the stem. The medial part of the encephalic cast is bounded ventrally by two hypocerebral processes (enclosing lmp in Pl. 6, fig. 2—*M. barrandei*) which almost, but not quite, meet at the mid-line. Above these, the middle part of the encephalic cast communicates with the thecal cavity by a medial part foramen (mpf in Pl. 6, fig. 4 and Pl. 6, fig. 2—*M. barrandei*) through which, by analogy with *Mitrocystites mitra* (p. 322), passed paired medial part nerves (mpn). Ventral to the hypocerebral processes the thecal cavity communicates with the lumen of the anterior stem. In *M. barrandei* (Pl. 6, fig. 2) and

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Fig. 19. *M. i. miloni*. Reconstruction of brain and cranial nerves. a. dorsal aspect ; b. anterior aspect of posterior part ; c. right aspect of left side. af = anterior furcation of palmate complex ; ap = anterior part of brain ; bc = buccal cavity ; csb = carrot-shaped body (lateral-line ganglion) ; csbn = nerve to carrot-shaped body (nerve to lateral-line ganglion) ; e = vestigial eye ; mp = medial part of brain ; mpn = medial part nerves (bases of optic nerves) ; n_0 = nerves emerging from posterior coelom near midline ; n_1 to n_5 = nerves of palmate complexes ; olo = olfactory openings ; pal = palmar nerve ; pb = pyriform body ; pc = peripheral canal ; pf = posterior furcation of palmate complex ; pp = posterior part of brain ; ppn = posterior part nerve ; r = rectum.

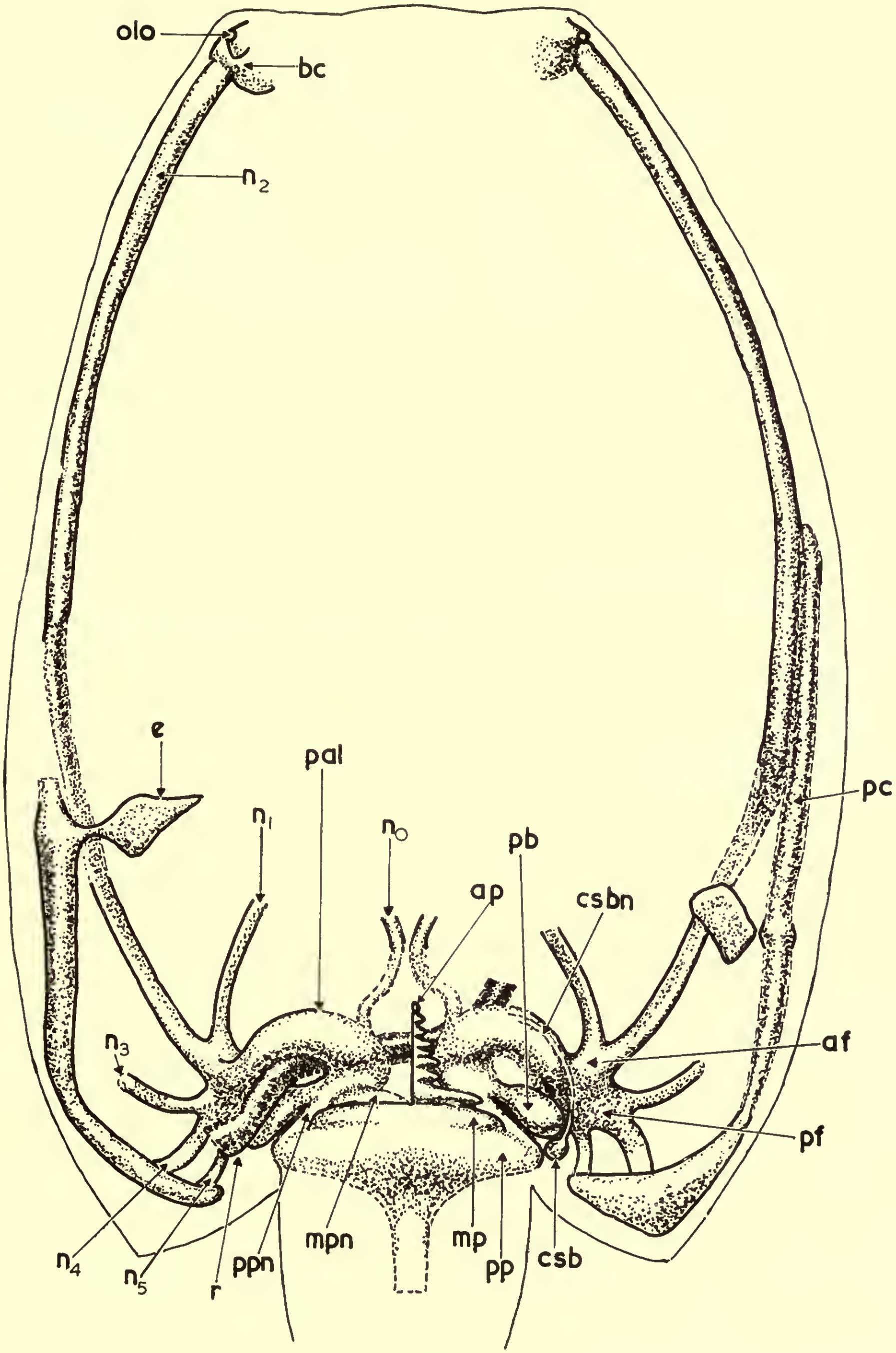
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Fig. 19.

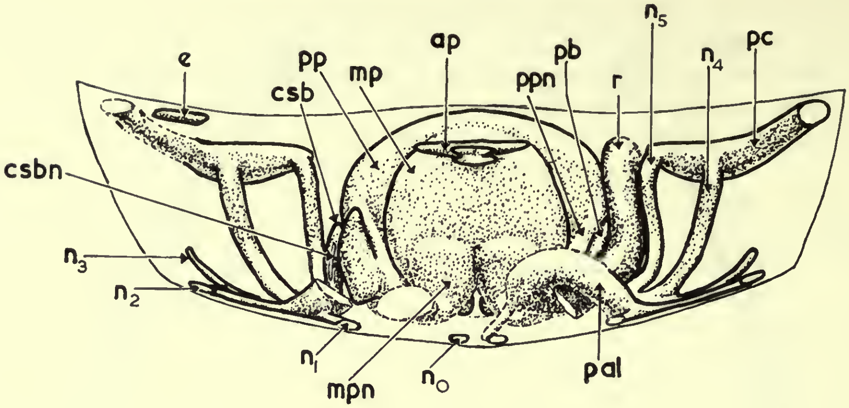

FIG. 19b.

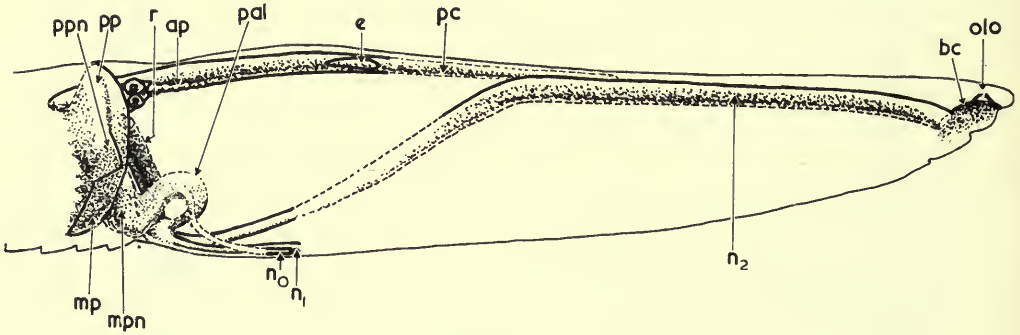

FIG. 19c.

Mitrocystites mitra (Pl. 9, fig. 6) the part of the encephalic cast enclosed by the hypocerebral processes is slightly swollen, so that a lower and an upper part of the medial brain (lmp, ump) can be distinguished. There are paired structures on the front of the posterior part of the encephalic cast, running towards the median plane and downwards (posterior part nerves, ppn in Pl. 6, figs. 2, 4).

The main structures related to the cranial nerves are as follows:

1. Right and left palmate complexes, so called because each consists of a trunk and five digitations. The proximal trunks (palmar nerve, pal in Fig. 19a–c; Pl. 5, figs. 6, 8; Pl. 7, fig. 1) first show themselves where they touched the anterior wall of the posterior coelom (Pl. 7, fig. 1) and, for some reason, caused the wall to calcify. The palmar nerves then entered the soft layer of the ventral skeleton at the ventral, anterior corners of the posterior coelom. After a short distance they divided into anterior and posterior furcations (af, pf in Fig. 19a–c; Pl. 5, figs. 6, 8). Each anterior furcation gave rise to two nerves (n_1, n_2) and each posterior

furcation to three nerves (n_3, n_4, n_5). The courses of these will be described when their nature is considered (p. 305). The left palmar nerve (Fig. 19c), judging by the trace that it left in the front wall of the posterior coelom, looped over the rectum before entering the ventral skeleton.

2. Right and left peripheral canals (pc in Fig. 19a–c; Pl. 5, figs. 3, 6; Pl. 6, fig. 7). These were spaces in the dorsal skeleton which were well developed on either side posteriorly and the right one can be traced at least as far forward as the suture $M_{3/4R}$. Both canals probably ended shortly in front of this. Posteriorly they they received nerves n_4 and n_5 of the palmate complexes.

3. Right and left " pyriform bodies " (pb in Fig. 19a, b; Pl. 5, fig. 6; Pl. 6, fig. 4; Pl. 9, fig. 1; Pl. 10, fig. 3) homologous with those of cornutes. These bodies lay as if pressed against the front faces of the posterior part nerves, but were actually separated from these by a thin layer of skeleton. They were totally enclosed in cupules in M_{1LD} and $_V$ and M_{1RD} and $_V$, except for a slit-like opening on the median side of each body.

4. A " carrot-shaped body " (csb in Fig. 19a, b; Pl. 5, fig. 6; Pl. 9, fig. 4; Pl. 10, fig. 3) just behind the right pyriform body. This underlay and communicated with the narrow groove (ng) on the surface of M_{1RV}. It received a laterally compressed nerve anteriorly (csbn in Pl. 10, fig. 3).

5. Right and left conical openings into the buccal cavity (olo in Fig. 19a, c; Pl. 5, figs. 7, 9).

6. Right and left nerves (n_0) that entered the soft layer of the ventral skeleton from the posterior coelom, near the mid-line (Pl. 5, fig. 11), within the plate V_{PM}.

It is interesting to compare the brain and cranial nerves of *M. i. miloni* with those of cephalaspids (Figs. 20, 21), for the latter are the only early Agnatha where these organs are known in detail. There is broad agreement that the brains of these fish much resembled that of *Petromyzon*, but there is unfortunately much difference of opinion as regards the cranial nerves.

The classical hypothesis of head segmentation has caused these differences of opinion, and therefore demands a digression. The version of the hypothesis expounded by Goodrich (1918, 1930) has been particularly influential (see e.g. de Beer 1937 : 15 ff.; Young 1950 : 144 ff.) and can suitably be explained here. According to Goodrich the branchial slits originally emerged between somites serially homologous with those of the trunk. Also there were " premandibular " and " mandibular " pairs of gill slits anterior to any now remaining, i.e. anterior to the spiracles of gnathostomes or to the homologous first branchial slits of Agnatha. Between the " mandibular " and " premandibular " pairs of gill slits lay the first prootic or " premandibular " pair of somites. These were associated with the trabeculae cranii, which represented the skeleton of an original " premandibular " branchial arch. Between the " mandibular " and the spiracular pairs of gill slits lay the second prootic or " mandibular " pair of somites, with which the mandibular skeleton was associated—originally as a gill arch, little different from the arches behind it. Between the spiracular and the first post-hyoidean gill slits lay the paired spiracular somites associated with the hyoid arch. The innervation of all interbranchial somites was supposed originally to have been like that of the trunk somites, with paired dorsal and ventral roots. The dorsal roots, however, would have had a strong branchial component. Accordingly, the first prootic ("premandibular") somites would have had the paired profundus branches of the trigeminal as their dorsal-root, branchial nerves, and would have had the oculo-motor nerves as their ventral roots. The second pair of prootic ("mandibular") somites would have had the rest of the trigeminal complex as their dorsal-root, branchial nerves, and the trochlear nerves as their ventral roots. The third pair of prootic somites would have had the facial nerves as their dorsal-root, branchial nerves and the abducens nerves as their ventral roots. The hypothetical ventral roots and paired somites associated with the first post-hyoidean arch have supposedly disappeared, but the glossopharyngeal nerves would have been the corresponding dorsal-root, branchial nerves. Each of the dorsal-root nerves going to the first few pairs of metotic somites supposedly had originally a branchial branch to the "corresponding" gill slit, but these branchial branches have since bunched together to form the paired vagus nerves. Consequently each metotic somite now has a ventral and dorsal spinal root nerve and is also, in theory, related to a branchial branch of the vagus. More detailed expositions of the hypothesis can be found in the cited works of Goodrich, de Beer and Young.

In considering this hypothesis, it must first be emphasized that branchiomerism and trunk segmentation are, of course, real phenomena. It is their supposed, original, simple relationship which is in doubt, and which has not everywhere been accepted (e.g. Romer 1949 : 555). Again, it is likely that the mandibular arch represents an original branchial arch, serially homologous with those behind it (e.g. Devillers 1958 : 573) and it is certain that the mandibular and maxillary branches of the trigeminal nerves were the original innervation of the mandibular and maxillary skeleton. It is very doubtful, however, that mandibular and premandibular gill slits ever existed, or that the trigeminal complex was originally branchial. Finally, the prootic somites are real entities which give rise to the oculo-motor muscles, and they are really innervated by the oculo-motor, trochlear and abducens nerves. But the serial homology of the prootic somites with the metotic somites or with the mesodermal pouches between the gill slits, the grouping of their nerves as ventral roots corresponding to dorsal roots represented by profundus, "true" trigeminal and facial nerves, and the separation of the prootic somites by hypothetical gill slits, are all baseless suppositions.

The arguments against the segmentation hypothesis in general, and Goodrich's version of it in particular, were forcefully marshalled by Kingsbury (1926). His case can be summarized as follows:

1. Gill slits seldom equal in number, and always appear later than and ventral to, the divisions between the trunk somites of the same region, and in amphioxus the gill slits do not even appear simultaneously on right and left sides. It may be added that there is certainly no serial relationship whatever between gill slits and trunk (i.e. tail) musculature in tunicate tadpoles.

2. The prootic somites differentiate, in general, from behind forwards, whereas the metotic somites, their supposed serial homologues, differentiate from in front backwards.

3. The nerves innervating the prootic somites, in particular the trochlear and abducens, do not have the central relations expected for somatic motor nerves, and do not pair with the profundus, " true " trigeminal and facial nerves as the hypothesis would require. The trochlear, in particular, always comes off the brain dorsally, after decussation of fibres.

4. The trigeminal nerves do not innervate gill slits in any living vertebrate.

5. The vagus nerve is never seen to be related to the spinal nerves in the way that the hypothesis suggests is primitive. In addition, the intestinal branch of the vagus will not fit into any segmental scheme. It may be added that the oldest-known vagus nerves—those of cephalaspids—are similar in morphology to the vagus nerves of living fish and agnathans.

Among recent works that adopt a segmentationist viewpoint, the contributions of Jarvik (1954 : 71 ff.), Bertmar (1959, esp. p. 341 ff.), Stensiö (1963, esp. p. 29 ff.) and Tarlo & Whiting (1965) should be mentioned. It is fair to say that all these authors, convinced that a segmentation scheme of Goodrich type was primitive, have tried to make the structures that they saw fit into it. The results are fairly plausible but not convincing enough to prove the truth of the scheme.

Jarvik, with great plausibility, serially homologised the elements of the mandibular arch in the crossopterygian *Eusthenopteron* with the elements of the hyoid arch and post-hyoidean arches behind. He also tried to recognise, but far less convincingly, the skeletal elements of a premandibular arch, anterior to the mandibular arch. Bertmar tried to do the same for certain Recent teleostean fishes. The account given by Jarvik (1954 : 71) of the views of previous workers is most revealing. For when authors such as Holmgren, Jarvik, Jaekel, Severtsoff and Allis, to name only some, disagree so completely, even as to the number of arches, it seems doubtful if such arches exist.

Stensiö (1963, esp. p. 29 ff.) elaborated the classical subdivision of the trigeminal complex, and wrote of paired trigeminal I and paired trigeminal II which he held to innervate mandibular and premandibular arches. Both pairs of trigeminals were supposedly provided, in cephalaspids, with dorsal sensory and ventral branchial branches. However, Stensiö gave no evidence of the existence of the paired dorsal branches of trigeminal II in cephalaspids (1963 : 29). Further, the interpretation of the other trigeminal branches (profundus, maxillary and mandibular), which careful reading shows to be identical to the interpretation of Wängsjö (1952), is not the most natural that can be offered.

Tarlo & Whiting (1965) reinterpreted certain paired pits inside the head shield of Cyathaspididae (Heterostraci). They saw in them indications of a complete series of head somites where previous authors had found indications of gill chambers. They also regarded the first two pairs of the pits that they figured as showing the positions of prootic somites. It is worth noting that Denison (1964 : 344) has, on good grounds, denied the existence of the first of these pairs of pits. Central to the argument of Tarlow & Whiting is the fact that the pits are sometimes striated approximately transverse to their axes, i.e. sub-parallel to the long axis of the animal. The authors therefore suggested that the striations cannot represent gill lamellae as Stensiö had suggested (1958 : 366) but must somehow be related to somites with fibres running parallel to the long axis of the animal. It is true that gill lamellae cannot be transverse to the direction of flow of water through a gill, but it is by no means obvious that the striations would be transverse to the direction of flow in Cyathaspididae, if the pits were occupied by gill pouches. Incidentally, the skeleton surrounding the gill chambers of Cephalaspididae shows very similar striations (see e.g. Stensiö 1958 : 197, fig. 115; 1963 : 33, fig. 16; Wängsjö 1952 : 159, fig. 15B). These also are roughly, though not accurately, transverse to the length of the gill chambers, but are nevertheless parallel to the likely direction of flow of water through the pharynx. In any case the distribution of the striations in cephalaspids, beginning just behind the peripharyngeal bands (Wängsjö, *loc. cit.*), shows that, whether or not they represent gill lamellae, they must certainly show the positions of gills. It is likely that they had the same significance in cyathaspidids. If interpreted as housing gill chambers, the first pairs of pits that exist (the second pair of Tarlo & Whiting) is not so far forward that it could not be homologous with the spiracular chambers of gnathostomes or the first gill chambers of Agnatha. Also, even if the pits housed interbranchial mesodermal pouches, as Tarlo & Whiting suggest, there is no sign that these pouches would form a continuous series with the trunk somites. The pits always cease just anterior to the branchial openings, and therefore well anterior to the back of the head shield (Denison 1964 : 345).

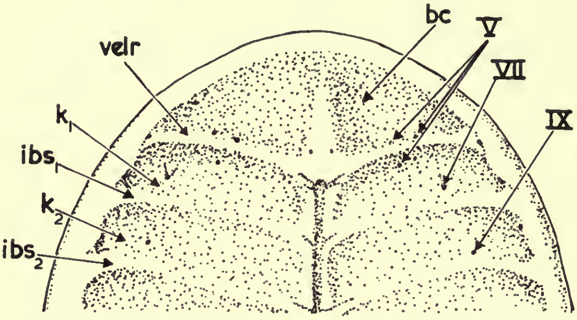

FIG. 20. Anterior part of roof of oralo-branchial chamber of the cephalaspid *Nectaspis areolata* Wängsjö. Redrawn after Wängsjö (1952, fig. 15c), relabelled. bc = buccal cavity ; $ibs_{1,2}$ = interbranchial septum ; $k_{1,2}$ = branchial pouches ; velr = velar ridge ; V, VII, IX trigeminal, facial and glossopharyngeal nerves.

Regarding cephalaspid cranial anatomy, there is a large oralo-branchial chamber in the head shield (Fig. 20) which is divided into a right and left series of smaller chambers. Stensiö (1927, 1958, 1963) maintained that all these smaller chambers carried branchial chambers. He also maintained (1927 : 167) that the division between the first and second chambers may have carried the velum, so that the first supposed pair of gill slits would be actually in front of the velum and would comprise perforations in the wall of the stomodeum. According to Stensiö the buccal cavity would correspond only to a small area at the extreme front end of the oralo-branchial cavity (dpr in e.g. Stensiö 1927, fig. 36). Wängsjö (1952, esp.

pp. 154 ff.), on the other hand, contended that the first pair of chambers (bc in Fig. 20) represented the buccal cavity, that the ridge behind it (velr in Fig. 20) supported the velum, as Stensiö had thought, and that only the chambers behind this ridge (k_1, k_2 in Fig. 20) were branchial. This second view is almost certainly correct. The chambers making up the first pair are clearly different from the chambers behind them (cf. Fig. 20, and e.g. Wängsjö 1952, fig. 15a, b, c). They lie in front of the distinct median groove in the roof of the oralo-branchial chamber made by the dorsal aorta. They never have the above-mentioned transverse striations which sometimes occur on the other chambers, and which probably indicate gills, and they never have any sign of branchial openings. Wängsjö (1952 : 135) described grooves in the skeleton for peripharyngeal bands, within the second pair of chambers, and the striations that indicate gills only occur behind these peripharyngeal grooves. This is exactly parallel to the situation in tunicates, amphioxus and ammocoete larvae. Further, Stensiö's belief in gills anterior to the velum is surprising from both hydrodynamic and comparative points of view, since the velum functions basically as a valve upstream of the gill slits and never has branchial slits anterior to it in any living chordate.

Stensiö (1927, 1958) originally maintained that the first pair of chambers (i.e. what is here interpreted as buccal cavity, bc in Fig. 20) received the right and left profundus branches of the trigeminal, which were thus branchial nerves. The second pair (k_1 in Fig. 20) received the " true " trigeminal nerves—also branchial. The third pair (k_2) received the facial nerves, the fourth (k_3) received the glossopharyngeal nerves, and fifth and succeeding chambers received successive branches of the vagus. His views, therefore, tallied well with classical segmentation theory.

Allis (1931) and Wängsjö (1952 : 63) disagreed with Stensiö's original views. They proposed instead that the profundus nerves were weakly developed and ran up through the orbits to the dorsal side of the head. Allis and Wängsjö held further that the nerves to the first pair of chambers (i.e. buccal cavity) were the maxillary branches of the trigeminal and the nerves to the second pair of chambers (i.e. first branchial chambers) were the mandibular branches of the trigeminal. In support of this latter contention Wängsjö cited the absence of swellings that might represent ganglia in the courses of these nerves to the first branchial chambers, which supposedly showed that they were motor nerves like the mandibular trigeminal nerves, but this argument is weak. Ganglia do not always show as obvious swellings of the nerves (cf. e.g. the reconstruction of the cranial nerves of *Petromyzon* by Johnston (1905, Pl. 5) especially the proximal, ganglionar part of the facial nerve) and still less as swellings in the nerve canals. As regards the nerves to more posterior pairs of chambers, Allis and Wängsjö agreed with Stensiö (1927). As already mentioned, Stensiö (1963 : 31) appears to have adopted Wängsjö's interpretation of the nerves to the first two pairs of chambers and of the profundus nerves.

A much more natural interpretation, however, was proposed by Lindström (1949 : 445). His interpretation of the profundus nerves agrees with that of Allis, Wängsjö and Stensiö (1963), i.e. he thought that they were weak, and innervated part of the dorsal surface of the head. For him, however, the paired nerves to the buccal cavity correspond to the whole of the rest of the trigeminal complex, since this supplies the mouth region in living agnathans and fish. The nerves to the first pair of branchial chambers were the facial nerves, for these supply the first pair of branchial chambers of living agnathans and the homologous spiracles of gnathostomatous fish. The nerves to the second pair of branchial chambers were therefore the glossopharyngeal nerves, and the nerves to the third and succeeding pairs of chambers were the branchial branches of the vagus. Lindström held that

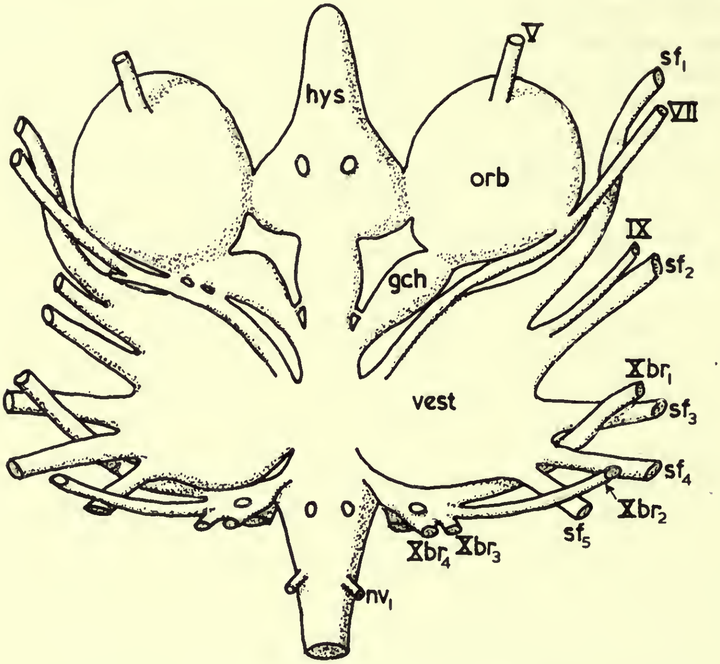

FIG. 21. Ventral aspect of canals associated with brain and cranial nerves of the cephalaspid *Nectaspis areolata* Wängsjö. Ventral aspect, redrawn after Wängsjö (1952, fig. 12), relabelled. gch = trigemino-lateralis chamber ; hys = hyphophysis ; orb = orbit ; sf = sensory field canals ; vest = vestibule ; V = trigeminal, VII = facial, Xbr_{1-4} = branchial branches of vagus.

the facial nerves left the brain anterior to the ear and ran through paired canals, the proximal parts of which were labelled l by Stensiö (1927 : 136, fig. 28). These canals touched the orbits in parts of their courses (cf. Fig. 21). The glossopharyngeal, according to Lindström, left the brain just behind the ear through the paired canals VIIIp of Stensiö (1927, fig. 28), and ran through the vestibule on their way to the second branchial chambers. Although, therefore, the points of origin and the end organs of the facial and glossopharyngeal were the same as in modern analogues, the intermediate courses of these nerves were somewhat different. Lindström, however, points out that this is not surprising, since the most anterior gill chambers of cephalaspids lay far forward relative to the brain, compared with modern analogues. There is, indeed, every reason to accept Lindström's interpretation which has been followed in labelling (Figs. 20 and 21).

Other points have been at issue in cephalaspid cranial anatomy. Thus the large paired chambers just behind the orbit (gch in Fig. 21) were regarded by Stensiö (1927) as myodomes for oculo-motor muscles. Wängsjö (1952 : 67 ff.) has shown that sometimes they are fusiform in shape and cannot therefore be myodomes. He identified them as chambers for the trigemino-profundus and anterior lateralis ganglia, and there seems little doubt that he was right.

Again, the well-known dorsal and lateral fields of cephalaspids were regarded as electric fields by Stensiö (1927), but Bohlin (1941), Westoll (1945) and Wängsjö (1952 : 192) thought they were sensory, largely on account of their thinness. They connected the fields, with some doubt, to the lateralis system. Watson (1954 : 20 ff.) elaborated a somewhat similar interpretation, pointing out that the so-called nerve canals (sf_{1-5} in Fig. 21) to the dorsal and lateral fields were much too wide to have carried only nerves. He suggested instead that they carried canals from the labyrinth and that the whole apparatus was a development of the ear that substituted functionally for the deficient lateralis system. Stensiö (1963 : 38) accepted that the fields in question were sensory fields of a special nature.

The brain and cranial nerves of *M. i. miloni* will now be compared with those of agnathans in general and cephalaspids in particular, assuming that the interpretations of the latter shown in Fig. 20 and 21 are correct.

The brain (Figs. 19a–c) resembles that of a lamprey or cephalaspid, except for being much shorter. The posterior part (pp) corresponds to the medulla oblongata plus the ventral part of the mesencephalon. The posterior part nerves (ppn) are the medullary nerves, presumably including equivalents of everything from trigeminal V to vagus X. Oculo-motor nerves (III, IV, VI) would not be represented as such, for there could be no oculo-motor muscles (cf. *Mitrocystites mitra* p. 319).

The medial part of the brain represents the optic lobes dorsally and the diencephalon more ventrally. The foramen (mpf) would be the outlet for the optic nerves (mpn). The whole of the medial part of the brain dorsal to the optic nerves would be optic in function. The part of the medial part of the brain just ventral and posterior to the optic nerves would, on vertebrate analogies, be functionally related to the hypophysis, which would have lain just beneath the gap between left and right hypocerebral processes. This lower medial part of the brain (lmp), in agreement with its different function, is differentiated from the optic, upper medial part (ump), as mentioned above, by being slightly protuberant in *Mitrocystella barrandei* and *Mitrocystites mitra.*

The anterior part of the brain (ap), which connected with the rest of the brain just dorsal to the optic nerves, would represent the telencephalon, with an olfactory function.

Turning to the palmate complexes, the anterior furcation (af) of each gave rise to n_1 and n_2 (Figs. 19a–c; Pl. 5, figs. 6, 8, 11). The courses of these within the median layer of the ventral skeleton, through most of M_{1L} and RV, are flanked by thickenings of the outer calcite layer (see especially Pl. 5, fig. 8). These thickenings suddenly stop anteriorly, but the nerves must clearly have continued beyond them. The nerves n_1 presumably ran forward and innervated the muscles inside the flexible ventral skeleton. The nerves n_2 presumably followed the lateral extensions of the soft layer out of the ventral skeleton (Fig. 15E, F) and can be traced again, after only a short interval, by means of right and left grooves in the skeleton corresponding to a ridge each side of the internal cast (n_2 in Pl. 5, fig. 1). The ridges run forwards into the buccal cavity (n_2 entering bc in Pl. 5, figs. 7, 9).

The nerves n_2 therefore compare at first sight with the nerves that innervate the buccal cavity of cephalaspids, i.e. the right and left trigeminal V, but further consideration refines this comparison. Thus Lindström has shown (1949 : 354, 384, 439) that the trigeminal complex of modern agnatha has paired maxillary and mandibular branches. The same may also have been true of cephalaspids, though direct evidence would not be expected since the relevant parts of the anatomy would be ventral to the dorsal shield. By comparison, therefore, it seems likely that the nerves n_1 of *M. i. miloni* correspond to the mandibular, and n_2 only to the maxillary branches of the trigeminal. The probable motor function of the nerves n_1 agrees with this supposition. The fact that the nerves n_2 innervated the ventral wall of the theca and the lower lip in *Mitrocystites mitra* (p. 322), and probably did so in *M. i. miloni*, does not argue against comparing them with the maxillary trigeminal nerves of cyclostomes, which behave similarly (Lindström 1949 : 439).

The posterior furcations of the palmar nerves (pf in Fig. 19a, Pl. 5, figs. 6, 8) gave rise to nerves n_3, n_4 and n_5 on each side. The positions of n_3 are defined on each side in the median soft layer of M_{1L} and RV by thickenings of the outer calcite layer. Their courses cannot be traced in the soft layer after the latter leaves the ventral skeleton. The nerves n_3 of *M. i. miloni* clearly correspond to n_3 of *Mitrocystites mitra* (p. 322), for in both species they lay between the nerves n_2 and the branchial openings. The nerves n_3 of *M. mitra* were clearly optic nerves leading to eyes resting on the sutures $M_{2/3R}$ and L and n_3 of *M. i. miloni* must be vestigial optic nerves. In many specimens of *M. i. miloni* the soft-tissue filled cavities of the dorsal skeleton flanking the sutures $M_{2/3L}$ and R show angular extensions (e in Fig. 19a–c; Pl. 5, fig. 3; Pl. 6, fig. 1) in much the same position as the eyes of *M. mitra*. These extensions may represent vestigial eyes.

Nerves n_4 and n_5 from the posterior furcations (Fig. 19a–c; Pl. 5, figs. 6, 8) can be followed through the median layer of M_{1L} and RV and into the posterior, dorsal extensions of this layer in M_{1L} and RD where, ultimately, they join the peripheral canals (pc in Figs. 19a–c; Pl. 5, figs. 3, 6; Pl. 6, figs. 1, 7). In both ventral and dorsal skeleton, their courses are flanked by thickenings of the outer layer of calcite. Nerves n_4 and n_5 are on each side median and posterior to the gill opening and cannot therefore be homologous with any part of the trigeminal complex of an agnathan or fish.

The peripheral canals, judging by their superficial position, were probably sensory, and n_4 and n_5 represent their nerve supply. It is possible that the peripheral canals are homologous to the sensory fields of cephalaspids, but equally possible that any resemblance is convergent. The possible homology would be inconsistent with the above-mentioned suggestions of Bohlin (1941), Westoll (1945) and Wängsjö (1942 : 192) that the sensory fields of cephalaspids might be related to the lateralis system, since in *M. i. incipiens* the lateralis system exists in a very primitive form (see below) and is not related to the peripheral canals. It would also be inconsistent with Watson's (1954) interpretation of these fields as elaborations of the ears, since the lateralis system of *M. i. miloni* was too primitive to include ears.

The palmar nerves, to judge by what comes off them peripherally, must have formed proximally by fusion of medullary nerves (posterior part nerves) and optic nerves (medial part nerves). This is reasonable since in *M. i. miloni, M. barrandei* and *Mitrocystites mitra* the posterior part nerves ran forwards, downwards and admedian, and in *M. mitra* direct evidence shows that the medial part nerves ran forwards, downwards and away from the median plane. They could, therefore, easily have fused shortly after leaving the dorsal skeleton.

The nature of the pyriform bodies, the carrot-shaped body behind the right pyriform body, and the narrow groove (ng) in M_{1RV} must be considered together. The pyriform bodies are reminiscent of the trigemino-lateralis chambers of cephalaspids (gch in Fig. 21) in position and their shape suggests that they carried ganglia. As mentioned above, however, Wängsjö (1952 : 67) has shown that the trigemino-lateralis chambers in cephalaspids carried both the trigemino-profundus and anterior lateralis ganglia. Bearing this in mind, it seems likely that the pyriform bodies correspond to trigemino-profundus ganglia alone, that the carrot-shaped body was a lateralis ganglion, that the groove that it underlay was the lateral line and that the canal emerging from the front of the body (csbn) carried a lateral-line nerve.

Several considerations support this view. Firstly, the right and left trigemino-profundus ganglia of *Petromyzon* lie just in front of the anterior lateralis ganglia, just as the right pyriform body lies just in front of the carrot-shaped body. Secondly, lateral-line ganglia are often peripheral in position. And thirdly, Pumphrey (1950) has shown that the acustico-lateralis system, on physiological grounds, must first have appeared as lateral-line.

As regards functioning, the groove (ng) of *M. i. miloni*, because of its position, would often be buried in mud, but this would not affect its efficiency as lateral-line, since the damping effect of half a centimetre of mud would be negligible. Pumphrey has shown (1950 : 7) that the great length of the lateral line in fish makes it possible to locate the position of sound sources. It is therefore interesting that in *Chinianocarpos thorali* the groove (ng) is represented only by a pit (personal observation) so that the system increased in length during the evolution of the Mitrocystitidae.

Comparison of the olfactory nerves and telencephalon with cephalaspids is of little help, since the olfactory opening of these fish lay on top of the head between the eyes. This is a highly unusual feature among vertebrates and corresponds to nothing in the mitrocystitids. A more helpful comparison is with Heterostraci. It is generally accepted that a right and left nasal sac opened downwards into the buccal cavity in these fish. Stensiö (1958) opposed this view, but Heintz (1962) argued convincingly in favour of it and refuted Stensiö's reconstructions.

It seems likely that the apices of the conical pits (olo) that open into the buccal cavity in *M. i. miloni* represent the points where the olfactory nerves entered the skeleton. The conical pits may themselves represent the nasal sacs of Heterostraci, but it is perhaps more likely that olfactory sensitivity was distributed over the whole dorsal wall of the buccal cavity, and the conical pits were simply the places where olfactory fibres converged before entering the skeleton.

The cavity containing the anterior part of the brain (ap) had numerous conical extensions to right and left. These extensions probably represent the places where olfactory fibres, or bundles of fibres, left the skeleton. The course of these fibres between the olfactory openings (olo) and the anterior part of the brain is conjectural. They may have passed through the short canals (sc) across $M_{2/3L}$ and $_R$ shown in Pl. 6, fig. 7, but, being very thin structures, they would not normally be traceable. The olfactory system of *M. i. miloni*, in any case, compares closely with that of Heterostraci except that the brain and olfactory sense organs were widely separated.

It is almost certain that the viscera, and very likely the gill slits, would need to be innervated from the brain in *M. i. miloni*. By comparison with vertebrates in general the corresponding nerves would be respectively the paired intestinal branches of the vagus, and the branchial branches of the facial, glossopharyngeal and vagus nerves, all of which, of course, arise from the medulla. With one likely exception there is no direct evidence of these nerves in *M. i. miloni*, but they could well have existed without touching the skeleton. The exception corresponds to the paired nerves n_0 to the ventral skeleton, which, by comparison with *Petromyzon* (Johnston 1905, pl. 5) may possibly represent the non-lateralis component of the hyomandi-

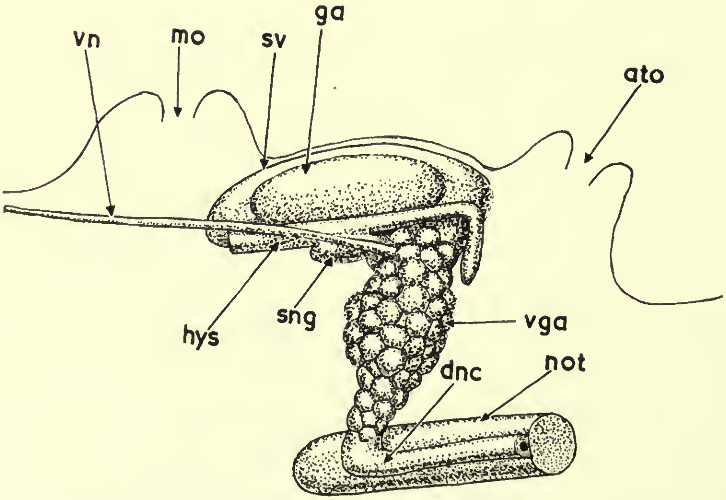

FIG. 22. Brain and associated structures of the tadpole larva of the tunicate *Amaroucium constellatum* (Verrill) (redrawn after Grave, 1921, fig. C). ato = atrial opening ; dnc = dorsal nerve cord ; ga = definitive ganglion ; hys = hypophysis ; mo = mouth ; not = notochord ; sng = subneural gland ; sv = sensory vesicle ; vga = visceral ganglion ; vn = visceral nerve.

bular branches of the facial. It is possible that the nerves n_0 also represent the median-line nerves of cornutes.

The hypophysis of *M. i. miloni* must, as already mentioned, have underlain the lower medial part of the brain (lmp) and have been connected to the buccal cavity by a duct, as it is in tunicates. In echinoderm terms it corresponds in position to the axial sinus plus the water vascular system, i.e. organs arising from the left axohydrocoel. The opening into the buccal cavity would correspond to the hydropore. The possibility of this homology was implied by Goodrich (1917).

It is interesting to compare the brain of *M. i. miloni* with that of a tunicate tadpole such as *Amaroucium constellatum* as described by Grave (1921) (cf. Fig. 22). This has a visceral ganglion posteriorly, which joins the dorsal nerve cord. Anteriorly are the sensory vesicle to the right, containing the eye and the statocyst, and the definitive ganglion to the left, in contact with the hypophyseal duct. A visceral nerve runs from the left, anterior corner of the visceral ganglion to the region in front of the oral siphon.

The visceral ganglion of a tunicate tadpole can be compared with the medulla oblongata of vertebrates and the posterior part of the brain of *M. i. miloni.* The visceral nerve corresponds in general to the nerves arising from the medulla, and therefore to the posterior part nerves. The sensory vesicle corresponds to the optic lobes, the optic part of the diencephalon, the optic nerves and the eyes of a vertebrate, and to the upper medial part of the brain, optic nerves (n_3) and eyes of *M. i. miloni.* The definitive ganglion corresponds to the hypophyseal part of the diencephalon of a vertebrate, and therefore to the lower medial part of the brain of *M. i. miloni.* Perhaps the most important differences in the nervous systems of tunicate larvae on the one hand, and vertebrates and mitrocystitids on the other, are the absence in tunicate tadpoles of telencephalon, olfactory nerves and acustico-lateralis system. These differences could easily be due to very small size. The statocyst is likely to be a specialization peculiar to tunicates, and functionally equivalent to the acustico-lateralis system.

In further connection with the optic system Dilly (1964) showed that the outer segments of the visual cells of tunicate tadpoles have fundamentally the same ultrastructure as those of vertebrates, indicating inheritance from a common ancestor. This was confirmed by Eakin (1965), who made a brief survey of the different types of photoreceptors described in the literature and showed how different from all others the tunicate tadpole or vertebrate type was. It is therefore not surprising that *M. i. miloni*, which must be close to the common ancestor of tunicates and vertebrates, had an optic system comparable both with that of a tunicate tadpole and with that of an agnathan.

In summary, it seems that the brain and cranial nerves of *M. i. miloni* fundamentally resembled those of vertebrates in general, and primitive agnathans in particular, and were also comparable with those of tunicate tadpoles. The trigeminal complex, trigemino-profundus ganglia, optic, lateralis and olfactory systems were already developed and the brain was divided into portions that are also recognizable in both fish and tunicate tadpoles.

POSTURE, FEEDING AND MOVEMENT: It is fairly certain that *M. i. miloni* habitually lay with the big-plated side upwards. The reasons are: firstly, this side corresponds morphologically to the upper side of cornutes (p. 289); secondly, it corresponds to the dorsal side of fish; thirdly, the probably sensory peripheral canals, and the eyes and peripheral grooves of *M. mitra*, were on this side; fourthly, in this position the more heavily armoured side would be upwards, which seems reasonable. The ventral parts of the theca would certainly be partly buried in the bottom.

The posterior stem, is commonly bent ventrally in the fossils as found and would have served as an anchor.

Feeding must have been microphagous, and the position of the mouth suggests a deposit feeder. Water was probably pumped through the pharynx by muscles internal to the flexible anterior ventral skeleton. This implies the existence of a velar valve across the posterior margin of the buccal cavity. Pumping by the ventral wall of the theca would not much disturb the mud beneath but would merely raise and lower the dorsal surface.

The anterior stem is seldom well-preserved in *M. i. miloni*, but could probably flex both vertically, by analogy with *M. barrandei* (p. 293), and horizontally, by analogy with *Mitrocystites mitra* (p. 322). The roughly symmetrical, tadpole-like shape of *M. i. miloni* suggests that the animal could swim forwards by lateral flexing of the anterior stem. The extensive, soft tissue-filled spaces in the skeleton may have assisted swimming by lightening the skeleton.

M. i. miloni could probably also crawl backwards pulled by the ventral flexing of the stem. A backwards direction of crawling is suggested by the direction of imbrication of anterior ventral plates (Fig. 13b; Pl. 4, fig. 8) and the transverse ridges (tr in Fig. 13b; Pl. 4, fig. 8), steeper anteriorly than posteriorly, which cross the posterior ventral part of the theca. Both these features would resist forward movement. Also the ventral muscles of the posterior stem were probably larger than the dorsal ones, suggesting that they delivered the power stroke.

The transverse ridges would be most useful when the animal, in crawling, pulled the posterior stem from the sea bottom. This would tend to push the theca anteriorly and also exert a turning moment on it, so that the postero-ventral surface, where the ridges are, would be driven hard into the mud. There are no yaw prevention structures (anterior appendages or ventral spikes) on *M. i. miloni*, which fact suggests that, in crawling, vertical flexing of the stem was more important than horizontal flexing.

d. ***Mitrocystites mitra*** Barrande

Systematic position: Family Mitrocystitidae (as *Mitrocystella*). Genus *Mitrocystites* Barrande 1887, species *Mitrocystites mitra* Barrande 1887, the type species. For an account of the systematics see Chauvel (1941).

Occurrence: Šarká Beds (Llanvirn Series) and Dobrotivá Beds (Llandeilo Series) of Bohemia. The most useful material, preserved in nodules, comes mainly from the Šarká Beds of Šarká, near Prague, and Osek, near Rokycany. The associated fauna indicates a shallow-water, marine environment.

MATERIAL: Národní Museum, Prague (about 220 specimens); British Museum (Natural History) (11 specimens, E 7517, E 16057–9, E 16061–3, E 16068–9, E 16089); University of Bonn (1 specimen); Museum of Comparative Zoology, Harvard (14 specimens Nos. 565 to 579); Royal Scottish Museum, Edinburgh (1 specimen) 1933.70.23; Sedgwick Museum, Cambridge (2 specimens) A48.926–7.

GENERAL SHAPE AND PLATE NOMENCLATURE: The general shape of *M. mitra* is very like that of *M. i. miloni* but broader. The sides of the theca are not so steep, but slope smoothly into the posterior ventral skeleton.

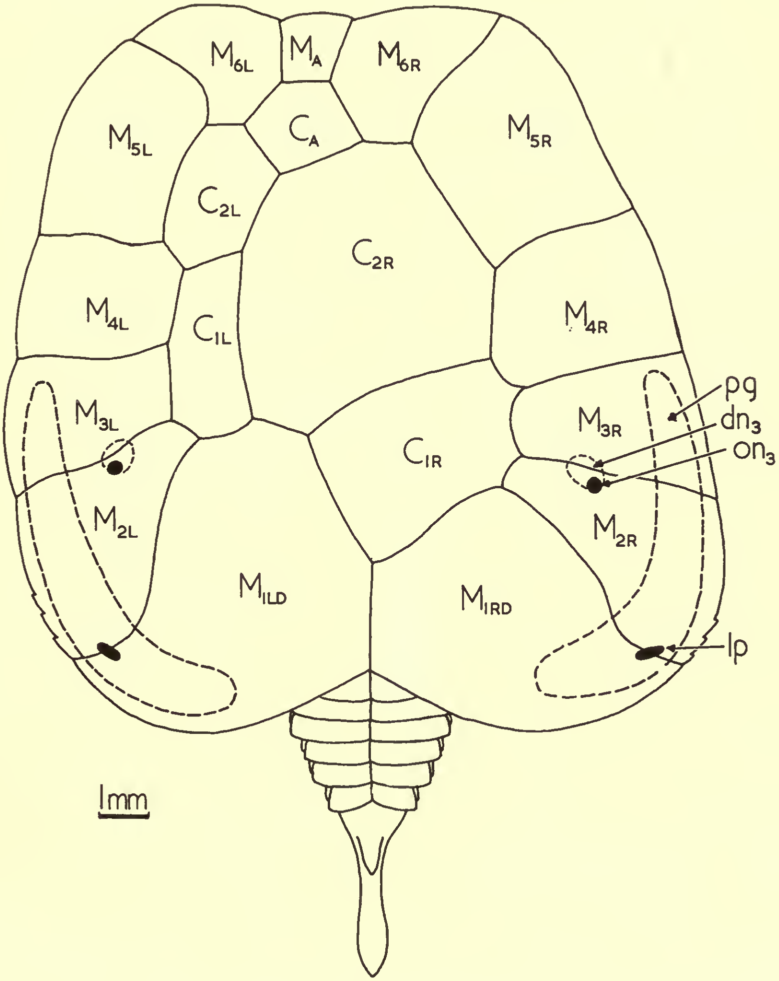

FIG. 23. *Mitrocystites mitra* Barrande. Reconstruction of external features. a. dorsal; b. ventral; c. right; d. anterior; e. posterior aspects. bo = branchial opening; dn_3 = depression associated with nerve n_3 (optic depression); lp = lateral pore; mo = mouth; ng = narrow groove (lateral line); on_3 = opening of nerve n_3 (optic nerve); or = oral plate; pg = peripheral groove; std = styloid; tr = transverse ridge.

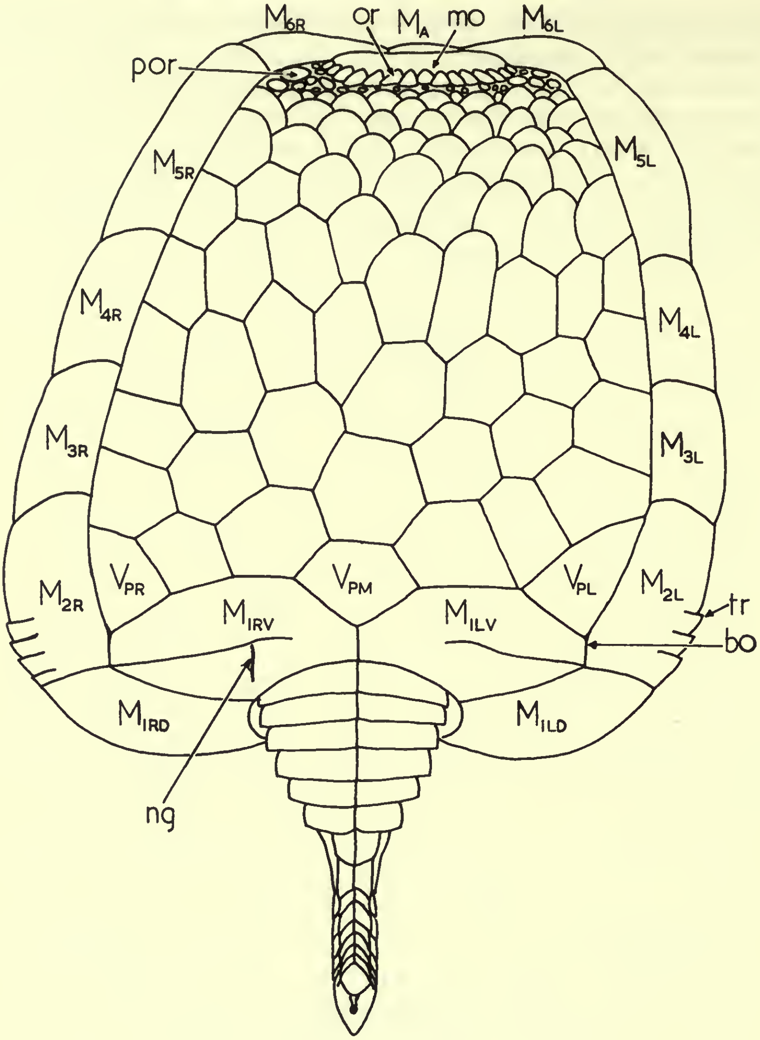
M6R
or
MA
mo
M6L
por
M5R
M5L
M4R
M4L
M3R
M3L
VPR
VPM
VPL
M2R
M2L
tr
bo
M1RV
M1LV
M1RD
M1LD
ng

FIG. 23b.

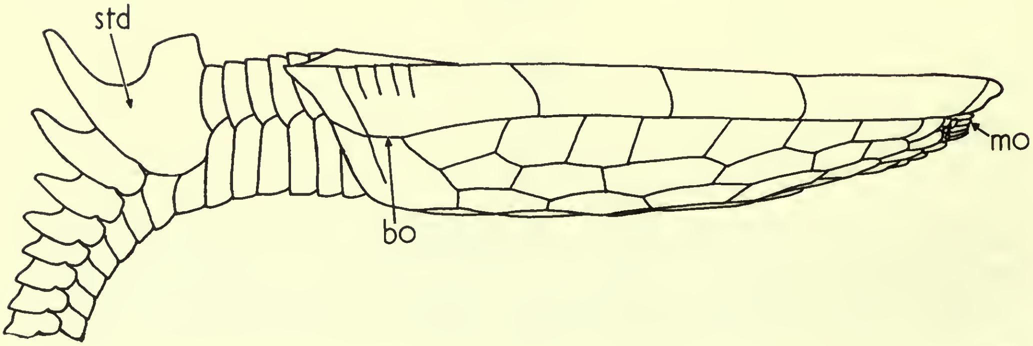

FIG. 23c.

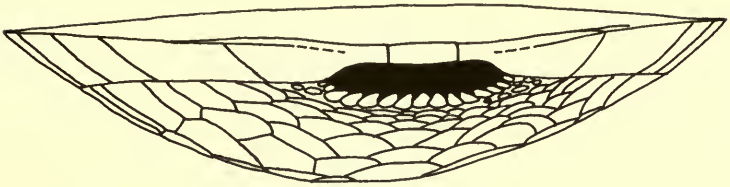

FIG. 23d.

The plates present in the theca are as follows:

Notation	Name	Homologous plate in *M. i. miloni*	
M_{1LV}	Left dorsal 1st marginal	M_{1LD}	
M_{1LV}	Left ventral 1st marginal	M_{1LV}	
M_{2L}	Left 2nd marginal	M_{2L}	
M_{3L}	Left 3rd marginal	? M_{3L}	(M_{3L} of *miloni* must correspond to either M_{3L} or M_{4L} of *mitra*, but it is not possible to say which)
M_{4L}	Left 4th marginal	? M_{3L}	
M_{5L}	Left 5th marginal	M_{4L}	
M_{6L}	Left 6th marginal	M_{5L}	
M_{A}	Anterior marginal	M_{A}	
M_{1RD}	Right 1st dorsal marginal	M_{1RD}	
M_{1RV}	Right 1st ventral marginal	M_{1RV}	
M_{2R}	Right 2nd marginal	M_{2R}	
M_{3R}	Right 3rd marginal	M_{3R}	
M_{4R}	Right 4th marginal	M_{4R}	
M_{5R}	Right 5th marginal	M_{5R}	
M_{6R}	Right 6th marginal	M_{6R}	
C_{1L}	Left 1st central	—	
C_{2L}	Left 2nd central	C_{L}	
C_{A}	Anterior central	C_{A}	
C_{1R}	Right 1st central	—	
C_{2R}	Right 2nd central	C_{R}	
V_{PL}	Left posterior ventral	V_{PL}	
V_{PM}	Median posterior ventral	V_{PM}	
V_{PR}	Right posterior ventral	V_{PR}	
—	ventral plates	ventral plates	

THECAL OPENINGS: The mouth is very like that of *M. i. miloni* but the oral plates, which number about fifteen, are shorter. The oral plates carry a hemicylindrical groove on their inner, dorsal faces (hg in Pl. 6, fig. 8) which may have housed a sphincter muscle.

The mouth opens distinctly leftwards in the smallest specimen seen (maximum thecal width 6·4 mm., Pl. 8, fig. 5), and makes an angle of about 12° with a line

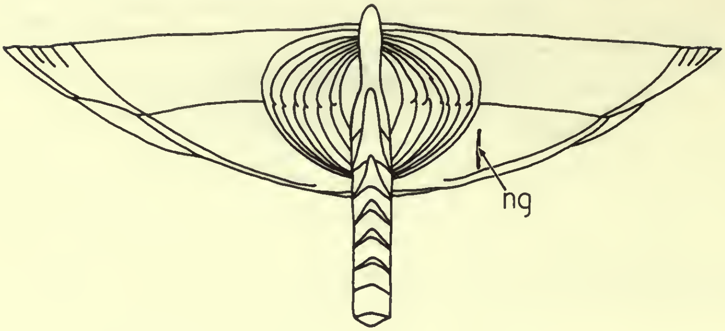

FIG. 23e.

joining the middle of the mouth to the middle of the cerebral depression. This asymmetry is absent from the largest specimens (e.g. Pl. 8, figs. 1, 8) and so, by extrapolation, was presumably even more marked during the earliest phases of life history, before a skeleton was acquired. The mouth also faced leftwards in adult *M. i. miloni* (p. 282, Pl. 5, fig. 2, about 5°) and *Chinianocarpos thorali* (Ubaghs, 1961*a*, fig. 1A, B, and personal observation, about 35°) and this is presumably a primitive characteristic of the Mitrocystitidae. It is interesting that the mouth also faces leftwards in larval amphioxus (e.g. Willey 1894 : 143 ff.).

The branchial openings were situated near the posterior right and left corners of the theca (bo in Fig. 23b, c and Pl. 8, figs. 2–4). Pl. 7, figs. 2, 4 show the plates associated with the gill opening on the left side of a single specimen. The break in slope (bsl) in these figures is not explicable if the plates M_{1LV}, M_{1LD} and M_{2L} were merely sutured together, and indicates that the apposed faces of M_{1LV} and M_{1LD}, posterior to the break in slope, were specialised to form articulation facets (af) dorsal and ventral to an articulation. Movement about this articulation would cause a gap to open between the left edge of M_{1LV}, anterior to the break in slope, and M_{2L}, above the gap. As in *M. i. miloni*, there was a median soft layer in the ventral skeleton, continuations of which entered the dorsal skeleton posteriorly and touched the inner faces of the dorsal skeleton laterally. The corresponding parts of the inner faces are excavated to receive the soft layer (sl in Pl. 7, fig. 4). It is apparent that the branchial openings would have been flanked by soft tissue which, as in *M. i. miloni* and *Cothurnocystis curvata*, would have acted as a seal when the opening closed.

The lateral line (ng in Fig. 23b, e, Pl. 8, fig. 3) is situated, as in *M. i. miloni*, on M_{1RV}.

On the dorsal surface are two pairs of openings not present in *M. i. miloni*. The more anterior of these (on$_3$ in Fig. 23a; Pl. 8, fig. 1; Pl. 10, figs. 5, 7, " paarige Gruben " of Jaekel 1918 : 121) are the openings of the optic nerves (n_3) on to the surface (n_3 are shown in Pl. 7, fig. 4; Pl. 8, fig. 10; Pl. 10, fig. 6). Each opening is often preceded by a small, paired depression across the suture $M_{2/3L}$ and R (dn$_3$ in Pl. 8, fig. 1) which presumably carried a vesicle on the end of n_3, i.e. an eye.

The more posterior pair of openings are termed lateral pores (lp in Fig. 23a, Pl. 8, fig. 1; Pl. 10 figs. 4, 5, " Seitenporen " of Jaekel 1918 : 121). They straddle the sutures M_{1LD}/M_{2L} and M_{1RD}/M_{2R}, and represent the openings on to the surface of nerves n_4 and n_5 (Fig. 27a, b, see also Pl. 6, fig. 6; Pl. 7, fig. 4; Pl. 8, fig. 4 and Pl. 10, fig. 6). The lateral pores are located at the deepest points of paired peripheral grooves (pg) which, though not sharply delimited, are situated near the posterior, dorsal edges of the theca. The peripheral grooves are evidently homologous with the peripheral canals of *M. i. miloni* which have the same position and innervation. The surface ornament of the plates is finer under the peripheral grooves than elsewhere (Pl. 10, fig. 5), indicating that in life the grooves probably contained soft tissue.

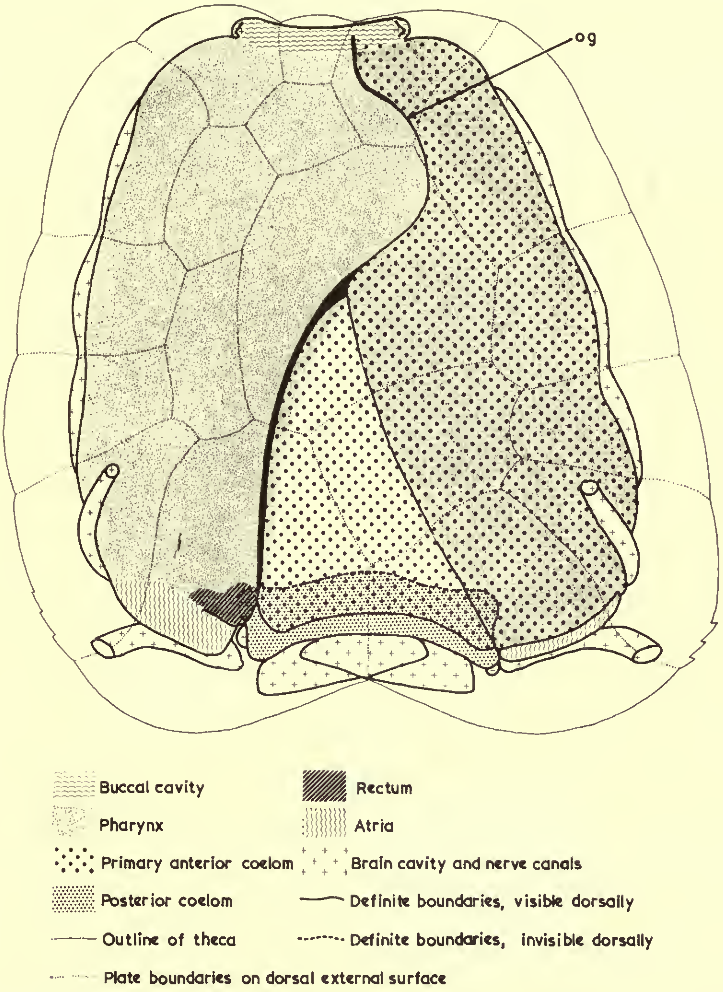
og
Buccal cavity
Rectum
Pharynx
Atria
Primary anterior coelom
Brain cavity and nerve canals
Posterior coelom
Definite boundaries, visible dorsally
Outline of theca
Definite boundaries, invisible dorsally
Plate boundaries on dorsal external surface

FIG. 24. *Mitrocystites mitra* Barrande. Chambers of the theca, dorsal aspect. og = oblique groove.

THE CHAMBERS OF THE THECA: The chambers of the theca differed very little from those of *M. i. miloni* but the intercameral ridges were less extensively calcified, so that relationships are generally not so well shown.

The oblique groove is basically similar to that of *M. i. miloni* but its anterior end is shallower (cf. Pl. 8, figs. 5, 10 with *M. i. miloni* in Pl. 5, figs. 7, 9). The median branch is well developed (mb in Pl. 8, fig. 10; Pl. 10, fig. 6). The oblique groove just posterior to it is not rounded in the way which, in *M. i. miloni,* suggests contact with the oesophagus (p. 285), but this need indicate only a very small difference in the position of the oesophagus. The separation (grp) between right pharyngeal chamber and residual anterior coelom shows clearly in Pl. 10, fig. 6. The part of the internal mould corresponding to the right pharyngeal chamber

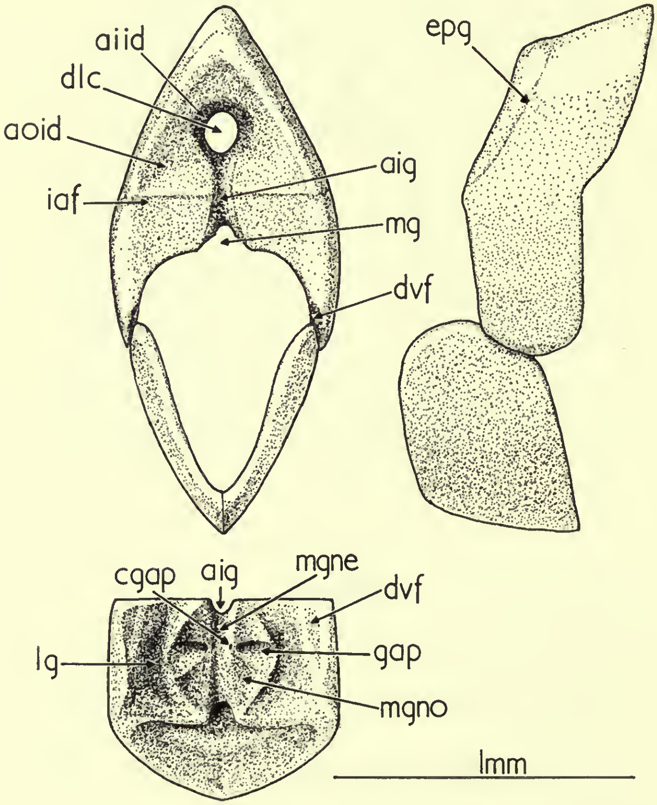

Fig. 25. *M. mitra.* Reconstruction of the skeleton of a segment of the posterior stem. a. anterior aspect ; b. left aspect ; c. ventral aspect of dorsal ossicle ; d. anterior aspect. aig = anterior interossicular groove ; aiid = anterior, inner interossicular depression ; aoid = anterior, outer interossicular depression ; cgap = canal leading to ganglionic pit ; dlc = dorsal longitudinal canal ; epg = epidermal groove ; dvf = dorsoventral facet ; gap = ganglionic pit ; iaf = interossicular articular facet ; lg = lateral groove ; mg = median groove ; mgne = neural part of median groove ; mgno = notochordal part of median groove ; pig = posterior interossicular groove ; piid = posterior, outer, interossicular depression ; poid = posterior,. outer, interossicular depression.

carries a series of weak corrugations (sp in Pl. 10, fig. 6) which are absent from the region corresponding to the anterior coelom. These corrugations are sometimes seen in the pharyngeal regions of the internal mould of *M. i. miloni* in large specimens (sp in Pl. 10, fig. 1), and can be compared with the striations on the walls of the pharynx in *Cothurnocystis elizae* (p. 257, sp in Fig. 3B, E; Pl. 2, figs. 2, 5). They may indicate folds in the wall of the pharynx, which would be appropriate for a respiratory and food-collecting organ.

The posterior coelom is very much as in *M. i. miloni*. The rectum, however, left it more anteriorly so that there is no rectal bridge. The rectal ridge is clearly visible (rr in Pl. 10, fig. 6). As in *M. i. miloni* the membrane limiting the posterior coelom seems to have been continuous with that limiting the left pharyngeal chamber. The two chambers were separated only by a fold in this membrane on the left side of the posterior coelom and this fold became less sharp anteriorly (Pl. 6, fig. 6; Pl. 8, fig. 10).

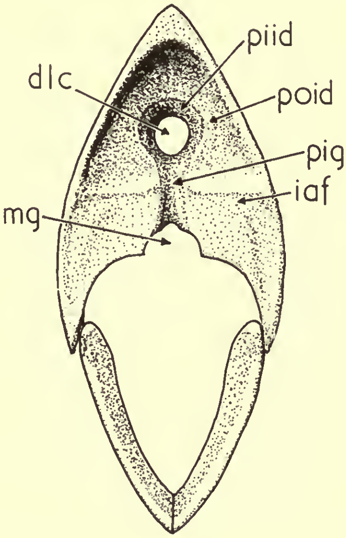

FIG. 25d.

The left atrium, perhaps because of the more anterior position of the rectum, shows more clearly than in *M. i. miloni* (la in Pl. 6, fig. 6; Pl. 8, fig. 10; Pl. 10, fig. 5). The right atrium is very like that of *M. i. miloni* (ra in Pl. 6, fig. 6).

The buccal cavity (bc in Pl. 8, fig. 10) was much as in *M. i. miloni*, but its wall was less extensively calcified, so that it cannot be dissected out of the internal cast. The olfactory openings (olo in Pl. 8, figs. 5, 10; Pl. 10, fig. 6) occupy exactly comparable positions.

THE STEM: This, again, much resembles that of *M. i. miloni*.

The posterior stem differs externally by having the dorsal ends of the ventral plates everywhere internal to the dorsal ossicles. Paired dorso-ventral facets on the internal face of the dorsal ossicles (dvf in Fig. 25a, c; Pl. 9, fig. 5) are found near the anterior, ventral corners of the ventral plates.

The soft parts are again reflected by the internal sculpture of the dorsal ossicles. The ventral surface of any one of these is traversed by a median groove (Fig. 25a, c) which is divided into an external, notochordal part (mgno) and a more median neural part (mgne). From the neural part a pair of canals goes off in each segment to ganglionic pits (gp). Anterior and posterior interossicular grooves are present in the median plane (aig in Pl. 8, fig. 4). The dorsal longitudinal canal is stouter than in *M. i. miloni*. The interossicular articulations are situated as in *M. i. miloni*. Anterior and posterior, inner and outer, interossicular depressions exist (aiid, aoid in Pl. 6, fig. 9; aiid, aoid, piid, poid in Fig. 23a, c, d). The outer depressions are shallower and wider than in *M. i. miloni* and the inner depressions relatively much smaller.

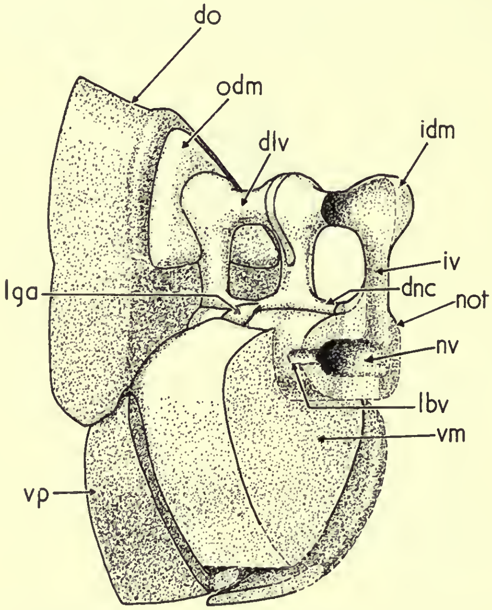

FIG. 26. *M. mitra*. Block diagram of posterior stem. dlv = dorsal longitudinal vessel; dnc = dorsal nerve cord; do = dorsal ossicle; idm = inner dorsal muscle; iv = interossicular vessel; lbv = lateral blood vessel; lgc = lateral ganglion; not = notochord; nv = notochordal vessel; odm = outer dorsal muscle; vm = ventral muscle; vp = ventral plate.

A natural mould of the ventral surface of the dorsal ossicles (Pl. 9, fig. 5) gives a representation of the soft parts. Here again a dorsal nerve cord (dnc) overlies a notochord (not) and gives rise to paired, pear-shaped ganglia (ga). In some parts of the specimen it can be seen that the ganglia were connected proximally to the dorsal nerve cord and not to the notochord.

The notochord was laterally compressed, where the apposed interossicular grooves came off but widened beneath the ganglia. Apposed interossicular grooves presumably carried an interossicular vessel going up through the dorsal nerve cord to a vessel in the dorsal longitudinal canal. The lateral widenings of the notochord may indicate lateral vessels coming off the notochord ventral to the skeleton. A reconstruction of the soft parts of the posterior stem is shown in Fig. 26.

Medial and anterior stems differ little from those of *M. i. miloni*, but the anterior stem had only six segments. On some specimens (Pl. 8, fig. 1; Pl. 10, fig. 7) the position of burial suggests that the anterior stem could flex from side to side.

The brain and cranial nerves: The skeletal histology of *M. mitra*, which affects the reconstruction of the cranial nerves, differs in some respects from that of *M. i. miloni*. Thus: 1. The median soft layer of the ventral skeleton (sl in Pl. 10, fig. 8) was not dilated where nerves passed through it. 2. All plates of the ventral skeleton, not only the more posterior ones, have an inner layer of calcite (il in Pl. 10, fig. 4). It can therefore be shown that there was no soft layer of connective tissue just within the outer calcite layer in the anterior ventral region. There is no evidence concerning this point in *M. i. miloni*. 3. There were no irregular, soft-tissue filled spaces in the dorsal skeleton. 4. As already mentioned (p. 315), the intercameral ridges were less extensively calcified than in *M. i. miloni*. 5. The outer surfaces of the central dorsal plates sometimes show near their centres (Pl. 8, fig. 1, fp.) a patch preserving the coarse fenestration of the juvenile skeleton (cf. Pl. 8, fig. 5 and the developing calcite plates of crinoids shown by Seeliger 1892).

Three of these features make the reconstruction of the cranial nerves more difficult than in *M. i. miloni*, namely the absence of dilatations in the ventral soft layer and of spaces in the dorsal skeleton, and the less extensive calcification of the intercameral ridges. Nonetheless, the two nervous systems were clearly very similar and the detailed differences are of much interest.

The anterior part of the encephalic cast is much smaller than in *M. i. miloni* (ap in Fig. 27a–c; Pl. 8, fig. 9), and takes the form of a crinkling of the median posterior dorsal suture ($\mathrm{M}_{1\mathrm{L/RD}}$). This crinkling is absent from all other sutures and is therefore unlikely to represent a mere strengthening device.

The medial part of the encephalic cast is more clearly demarcated in dorsal aspect from the posterior part of the cast than in *M. i. miloni* (Fig. 27a; Pl. 6, fig. 6; Pl. 8, fig. 10; Pl. 10, fig. 6; cf. Pl. 6, fig. 1; Pl. 10, fig. 3 for *M. i. miloni*). Its foramen (mpf in Fig. 27b, Pl. 9, fig. 6) is much wider than in *M. i. miloni* (Fig. 19b; Pl. 6, fig. 4) and grooves on the front of the hypocerebral processes (gmpn in Pl. 8, fig. 6) indicate the proximal courses of the medial part (optic) nerves. It therefore follows that the optic part of the brain and the bases of the optic nerves were relatively bigger in *M. mitra* than in *M. i. miloni*. This recalls that, more peripherally, the optic nerves (n_3) were much bigger in *M. mitra* and continued on to the dorsal surface of the theca, where each one ended in a vesicle or eye. In *M. i. miloni*, on the other hand, the eyes, if they existed at all, were only vestigial and the optic nerves, at least in the adult, did not connect with them. All parts ascribed to the optic system were therefore better developed in *M. mitra* than in *M. i. miloni*, which confirms that they had a common function.

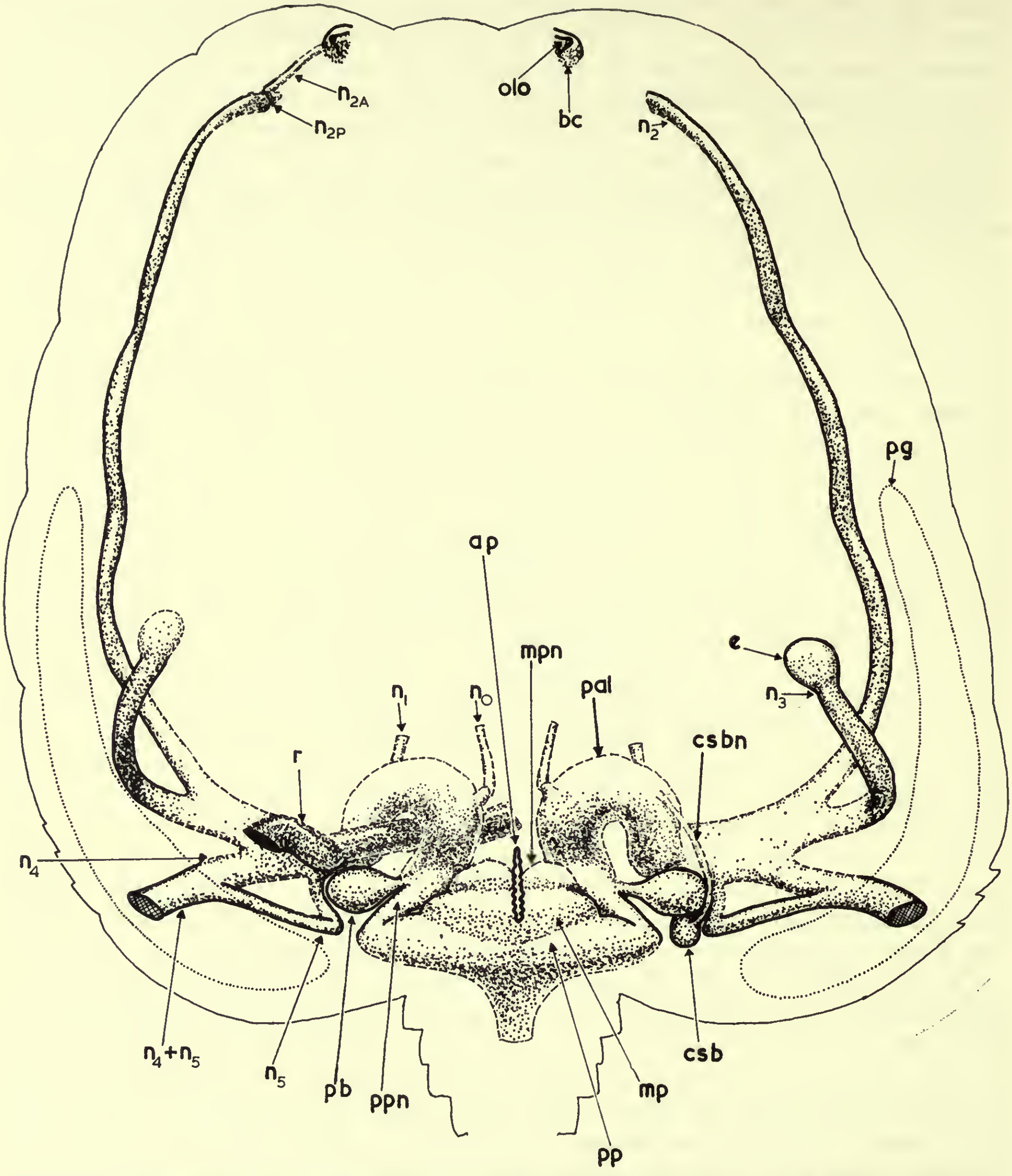

FIG. 27. *M. mitra.* Reconstruction of brain and cranial nerves. a. dorsal aspect; b. anterior aspect of posterior part; c. left aspect for right part; ap = anterior part of brain; bc = buccal cavity; csb = carrot-shaped body (lateral line ganglion); csbn = nerve to carrot-shaped body (nerve to lateral line ganglion); e = eye; lmp = lower medial part of brain; mp = medial part of brain; mpf = medial part foramen; mpn = median part nerves; n_0 = nerve leaving posterior coelom, near mid line; n1, 2A, 2P, 3, 4, 5 = nerves of palmate complex; olo = olfactory opening; pal = palmar nerve; pb = pyriform body; pg = peripheral groove; pp = posterior part of brain; ppn = posterior part nerve; r = rectum; ump = upper medial part of brain.

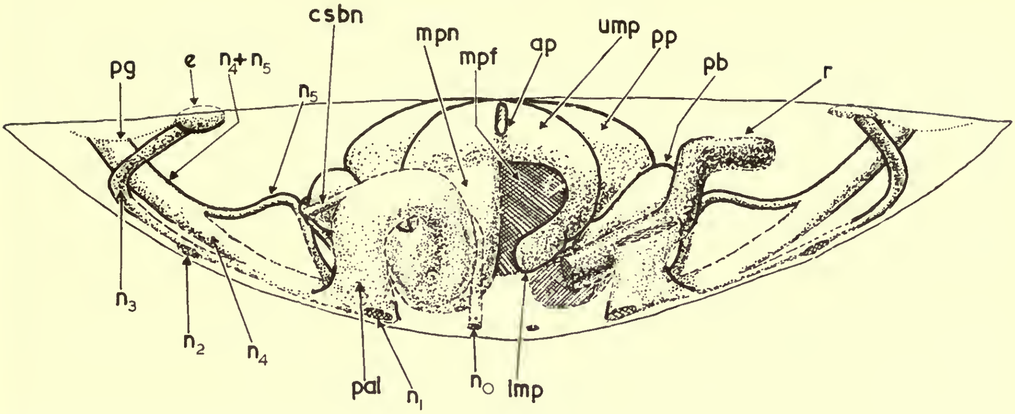

FIG. 27b.

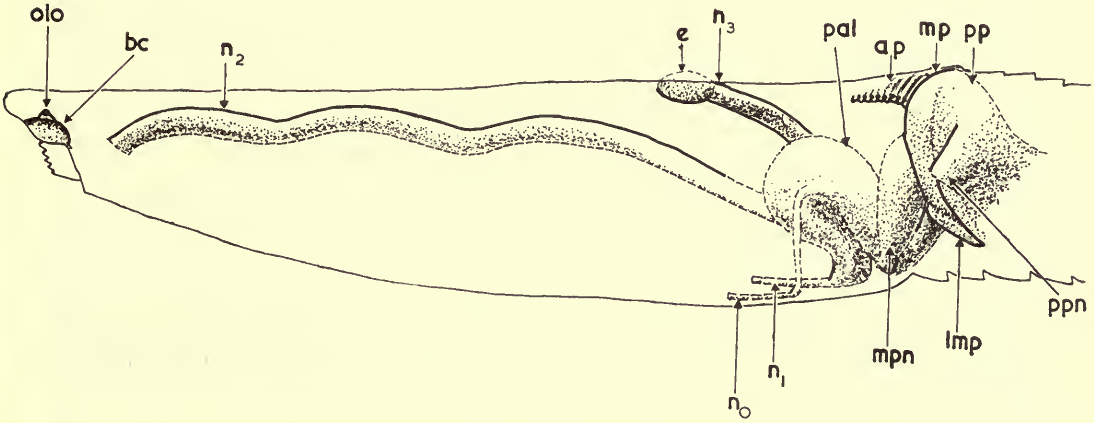

FIG. 27c.

The lower medial, or hypophyseal, part of the encephalic cast, as already mentioned, is slightly swollen in *M. mitra* (Pl. 9, fig. 6) differentiating it from the optic part of the encephalic cast.

The posterior part of the encephalic cast scarcely differs from that of *M. i. miloni.*

Turning to the palmate complexes, the palmar nerves (pal in Fig. 27a–c) did not cause the front wall of the posterior coelom to calcify so extensively as in *M. i. miloni* and consequently these nerves cannot be traced until they had already begun to enter the ventral skeleton. Their courses at these points were nearly vertical (pal in Pl. 10, fig. 8) as in *M. i. miloni,* and the left one presumably looped over the rectum as in that form.

Of the branches arising from the palmar nerves, left and right n_1, because of the absence of dilatations in the ventral, soft layer, cannot be demonstrated in *M. mitra,* though they doubtless existed. The nerves n_2 are most proximally indicated in one specimen (Pl. 10, fig. 8) just before the left one left M_{1LV}. They must have run through V_{PL} and $_{R}$ and left the ventral skeleton with the soft layer. They can be traced again on the inner faces of M_{2L} and $_{R}$ and then followed a course indicated by left and right grooves in the skeleton, much as in *M. i. miloni*. Anteriorly the grooves turn abruptly downwards in the middle of M_{5L} and $_{R}$, and at these points the nerves must normally have left the dorsal skeleton. In one specimen, however, the left groove bends horizontal again and runs forward as far as the anterior end of M_{5L} (Pl. 8, fig. 10). This suggests that left n_2 divided into two branches (n_{2A} and n_{2P} in Fig. 27a). n_{2P} was thicker and innervated the anterior part of the belly. n_{2A} was thinner and probably innervated the mouth and lower lip. The parts of the ventral skeleton innervated by these two branches can be estimated by comparing Pl. 8, fig. 8 and Pl. 8, fig. 10. There is no evidence as to whether right n_2 had comparable branches at its anterior end.

The nerves n_3 of the palmate complex, or optic nerves, can in one case be traced for a short distance in the ventral skeleton on the left side (Pl. 10, fig. 8). The canal which here carried left n_3 was compressed in section. The nerves n_3 left the ventral skeleton with the soft layer (Pl. 7, fig. 4) anterior to the branchial opening. They then travelled upwards and forwards in paired grooves (Pl. 6, fig. 6; Pl. 7, fig. 4; Pl. 8, fig. 10 and Pl. 10, fig. 6) which gradually deepened, leading finally to short cylindrical canals (Pl. 7, fig. 4) that opened (on3) on the dorsal surface. The changes in section of the nerves n_3—compressed in the ventral skeleton, becoming circular peripherally—strongly confirm that the structures were indeed nerves.

The two pairs of nerves n_4 and n_5 must have had courses in the median layer of the ventral skeleton very similar to those in *M. i. miloni*, though their exact positions cannot be defined. The nerves entered M_{1L} and $_{RD}$ with the median soft layer, much as in *M. i. miloni*. Immediately afterwards the nerves n_5 swung outwards to join n_4 (Fig. 27a, b; Pl. 8, fig. 10; Pl. 10, fig. 6) and n_4 and n_5 then on both sides ran upwards together, into the lateral pores, to innervate the peripheral grooves.

The pyriform bodies and lateral-line ganglia are much as in *M. i. miloni* except that the pyriform bodies were more symmetrical. The dorsal and ventral cupules enclosing the left pyriform body show in Pl. 8, figs. 2, 4. The lateral-line ganglion (csb) is shown in Pl. 10, fig. 8.

The olfactory nerves must have consisted, as in *M. i. miloni*, of isolated fibres in the dorsal skeleton connecting the olfactory openings (olo) in the buccal cavity with the telencephalon (ap).

The nerves n_0, in the absence of dilatations of the ventral soft layer, cannot be demonstrated in *M. mitra* but no doubt existed.

In summary, therefore, some features of the cranial nerves show more clearly in *Mitrocystites mitra* than in *M. i. miloni*. These features relate mainly to the optic system, the anterior end of the left maxillary trigeminal (n_3) and the hypophyseal part of the brain (lmp). Some details of the dorsal sensory complex (i.e. peripheral grooves and n_4 and n_5) also differ.

Posture, feeding and movement: *M. mitra* must have resembled *M. i. miloni* in posture, feeding and movement. Some specimens (Pl. 8, fig. 1; Pl. 10, fig. 7) show more clearly than in *M. i. miloni* that the proximal stem could bend from side to side. The theca probably lay more deeply buried in the mud than that of *M. i. miloni* since there is no sharp " change in slope " between marginal plates and posterior ventral skeleton, and the transverse ridges are restricted to the higher parts of the theca. The theca of *M. mitra* can be compared with the shell of the Recent bivalve *Pecten maximus*, which habitually lies with the convex valve downwards, and with the flat valve about level with the sea-floor.

IV. DISCUSSION

a. *Cornutes and Mitrates*

The imperfection of the fossil record makes it impossible to reconstruct the phylogeny of cornutes and mitrates in detail. Only one species of cornutes is known from the Middle Cambrian, whilst none is known from the Upper Cambrian. Five specimens (placed in two species and genera) are known from the Lower Tremadoc Series (Ubaghs 1963). In the Upper Tremadoc the cornute record is better but incomplete, since only one specimen is known from outside Europe (Gigout 1954). The only later cornutes described in the literature are those from the Ashgill Series of Scotland.

The record of the earliest mitrates is little better. The two earliest families, the Lagynocystidae and Mitrocystitidae, are both first known from the Upper Tremadoc or Lower Arenig Series. The species which represent those families at this horizon (*Peltocystis cornuta* Thoral and *Chinianocarpos thorali* Ubaghs) resemble each other enough to suggest a common origin from the cornutes. They also differ enough to indicate a long, unrecorded period of divergence. In later rocks the mitrates are fairly common, though they have not received much attention.

Nonetheless certain deductions concerning the phylogeny of cornutes and early mitrates are possible, despite this lack of fossils. Firstly, the cornutes and mitrates are certainly closely related to each other, and the establishment of a group to contain both (Class Stylophora, Subphylum Calcichordata) is justified. Secondly, the mitrates certainly arose from the cornutes, rather than the converse. Thirdly, the line of descent from the earliest known cornute (*Ceratocystis*) to *Mitrocystites* and *Mitrocystella* can be postulated from known forms. This reconstructed line of descent is essentially a working hypothesis, and although not entirely consistent with the stratigraphical order of first known occurrences, one must keep in mind the patchy fossil record. The Lagynocystidae are not further considered here, and until they have been studied in detail it is pointless to fit them into a general scheme.

The close relationship of cornutes and mitrates is indicated by a number of features in common: 1. Both groups had a mouth near the front end of the theca. 2. In both groups the skeleton was made of plates, each a single calcite crystal. 3. Both groups had a flattened theca, adapted for lying on the sea-floor, with dorsal and ventral surfaces. 4. Both groups had marginal plates, usually numbering twelve to fifteen, round the theca. Thus, counting dorsal and ventral first marginals, but excluding appendages, *C. elizae* had thirteen marginals, *C. curvata* had twelve, *Chinianocarpos thorali* had twelve, *M. i. miloni* had fourteen and *M. mitra* fifteen.

5. Both groups had a basically similar arrangement of thecal chambers. 6. Both groups had a brain and paired pyriform bodies at the anterior end of the stem. 7. In both groups the stem ended abruptly. 8. In both groups an anterior, tetraserial part of the stem was adapted for flexing sideways and a posterior part for flexing vertically. 9. Within the stem, both groups certainly had segmented muscle blocks and a chambered organ or notochord and both almost certainly had a peduncular nerve (dorsal nerve cord). 10. Both groups were pharyngotrematous. Cornutes had external branchial slits; Mitrates had presumed internal branchial slits and branchial openings. 11. Most cornutes had the anus, either internal or external, hust left of the stem while mitrates had the anus internal and just left of the stem. Against this, however, the earliest known cornute (*Ceratocystis perneri*) had the anus right of the stem (personal observation).

That mitrates were descended from cornutes, rather than the converse, is indicated by the fact that: 1. The earliest known cornute is Middle Cambrian in age, while the earliest known mitrates are Upper Tremadoc or Lower Arenig Series. 2. The mitrates give the impression of imperfect bilateral symmetry, imposed on a basic, cornute-like asymmetry. 3. One of the earliest known mitrates (*Chinianocarpos thorali*) has many cornute-like features, i.e. big plates just ventral to the mouth, a partly flexible thecal roof, an oblique groove borne entirely on marginal plates, not very massive dorsal stem ossicles, the ability to flex the posterior stem upwards, and a very short lateral line. The mitrates probably arose from the cornutes during the Upper Cambrian.

The line of descent from *Ceratocystis* to *Mitrocystites* and *Mitrocystella* can be reconstructed as follows:

1. *Ceratocystis*. Theca boot-shaped, rigid. Anterior appendages present. Anus external, right of the stem. Gill slits external, left of the stem. No lateral line. Only known occurrence, Middle Cambrian (*Ceratocystis perneri* Jaekel).

2. *Cothurnocystis* (*americana* type). Theca boot-shaped. Floor of theca rigid. Roof of theca a flexible integument. Anterior appendages not known. Anus not known. Gill slits external, left of stem. No lateral line. Only-known occurrence, Lower Tremadoc Series.

3. *Cothurnocystis* (*elizae* type). Theca boot-shaped. Floor of theca an integument crossed by a strut. Roof of theca a flexible integument. Anterior appendages present. Anus external, left of the stem. Gill slits external, left of stem. No lateral line. First known occurrence, Upper Tremadoc or Lower Arenig Series (*C. primaeva* Thoral).

4. *Phyllocystis*. Theca leaf-shaped. Floor of theca an integument crossed by a thin, curved and probably functionless strut. Roof of theca a flexible integument. Anterior appendages absent. Anus external, left of the stem. Gill slits external, left of the stem. No lateral line. First known occurrence Lower Tremadoc Series (*Phyllocystis* sp., Ubaghs 1963).

5. *Chinianocarpos*. Theca leaf-shaped. Floor of theca an integument with no strut. Roof of theca mainly rigid, with a small area of integument. Anterior appendages absent. Anus internal, left of stem. Gill slits internal, paired. Lateral line a small pit. Only known occurrence Upper Tremadoc or Lower Arenig Series (*C. thorali* Ubaghs 1961*a*).

6. *Mitrocystites* & *Mitrocystella*. Theca leaf-shaped. Floor of the theca an integument with no strut. Roof of theca entirely rigid. Anterior appendages absent. Anus internal, left of stem. Gill slits internal, paired. Lateral line a groove. First known occurrence Llanvirn Series (*Mitrocystites mitra* Barrande and *Mitrocystella barrandei* Jaekel).

The line of descent represented by *Cothurnocystis curvata* probably arose from a *C. elizae*-like ancestor. In most respects *C. curvata* differs more from *Ceratocystis perneri* than does *C. elizae*. Thus, unlike both *C. perneri* and *C. elizae*, *C. curvata:* 1. Has no right oral appendage. 2. The anus is internal. 3. The mouth is dorsal, instead of anterior. 4. The anterior margin is strongly convex upwards. 5. The stylocone tapers very abruptly. In addition, the branchial skeleton of *Ceratocystis perneri* needs little modification to produce that of *C. elizae*. It needs much modification, on the other hand, to produce that of *C. curvata*. The earliest-known representative of the *C. curvata* group, like that of the *C. elizae* group, is Upper Tremadoc or Lower Arenig in age (Ubaghs, personal communication). The internal anus may be a genuine point of comparison with mitrates, or may have been acquired independently.

The changes involved in going from *Cothurnocystis* of *elizae* type, through *Phyllocystis* and *Chinianocarpos* to *Mitrocystites* or *Mitrocystella* are worth stating in detail, since this course of evolution includes the origin of mitrates from cornutes.

1. *Mouth*

i. A big plate (M_A) developed dorsal to the mouth, as in *C. thorali*.

ii. Subsequently the big plates forming the ventral mouth frame (M_{5R}, M_{6L} of *C. elizae*, M_{5R}, M_{4L} of *C. thorali*) became reduced, so that they no longer met at the mid-ventral line. At about the same time M_A fused to these same plates.

iii. Presumably later than (i), the oral plates of the upper lip were lost.

2. *Thecal shape and skeleton of theca*

iv. Appendages and anterior ventral spikes were lost, as in *Phyllocystis*.

v. At about the same time the theca became more symmetrical, as in *Phyllocystis*.

vi. Somewhat later than (iv) and (v) the posterior, ventral spikes were lost. They are present but weak in *Phyllocystis*.

vii. The strut, which had functioned to prevent collapse of a concave anterior margin when the muscles of the integuments contracted, was lost. When this margin became convex, the strut lost its function. In *Phyllocystis* it is, accordingly, very slender and curved. It is absent in *Chinianocarpos thorali* where, as compared with *Phyllocystis*, the roof of the theca is more rigid and the floor is not in one plane.

viii. The marginal plates grew forward from the posterior, right-hand part of the theca, carrying the oblique groove with them, as in *C. thorali*.

3. *Thecal chambers and gill slits*

ix. The right pharyngeal chamber pouched out from the left one, and right gill slits appeared. In addition the right atrium and gill opening appeared, if the gill slits were already internal.

x. The pharyngo-visceral line (oblique groove) and anterior coelom came to be fixed to the ceiling of the theca. This could have been either the precondition for, or the result of, the appearance of the right pharyngeal chamber (ix). It was connected with the expansion of the right, posterior, marginal plates (viii).

xi. The atria appeared. Right and left atria probably arose simultaneously if the right gill slits had appeared already (ix). Otherwise the left atrium preceded the right one.

4. *Stem*

xii. The posterior stem developed the ability to flex downward as well as upward.

xiii. In connection with this, the ventral posterior stem ossicles became less massive and were finally reduced to paired ventral plates, and the stylocone disappeared. Conversely, paired dorsal plates fused, giving rise to massive ossicles. Interossicular articulations appeared, and then, later, the styloid arose by fusion of the two most anterior of these ossicles.

xiv. Subsequently the posterior stem lost the ability to flex upwards.

5. *The brain and cranial nerves*

xv. The first dorsal marginals enlarged and grew backwards, so enveloping the front of the brain and the dorsal sides of the pyriform bodies.

xvi. At about the same time the first ventral marginals became separated from the brain, though they retained contact with the pyriform bodies.

xvii. The optic nerves pushed upward and opened on to the dorsal surface.

xviii. The lateral line and its nerve supply appeared.

xix. The palmate complexes either arose or, as seems more likely, became enclosed in skeleton.

xx. The olfactory system either arose or became enclosed in skeleton.

Changes in the stem and theca can be explained by changes in the manner of movement. When an animal like *C. elizae* crawled backwards by sideways flexing of the anterior stem, the anterior rigid appendages and the ventral spikes prevented yaw and resisted forward slipping (p. 265). Such a form as *Phyllocystis*, with weak, posterior ventral spikes, a symmetrical theca and no anterior appendages or anterior ventral spikes, probably crawled backwards by flexing the anterior stem downwards, so pushing the rather stiff posterior stem anteriorly and ventrally into the mud. Yaw prevention devices would not be needed and were lacking. The weak posterior ventral spikes would function during the return stroke of the stem, which would exert a turning moment on the theca. This moment would push the posterior theca, where the spikes were, into the mud and prevent the theca from slipping forwards.

The mitrate ability to flex the posterior stem ventrally, with all its related changes, developed because this helped the anterior stem in the work of pulling the theca backwards. The transverse ridges on the postero-ventral surface of the theca of mitrates served the same function as the posterior ventral spikes of *Phyllocystis*.

In conclusion, the broad way in which cornutes and mitrates are related is fairly clear. Large morphological gaps remain to be filled, however, partly by new collecting, and partly by re-examining old material.

b. *Stylophora, echinoderms, hemichordates and chordates*

The relations of Stylophora with other groups, and the proposal to transfer them from the Echinodermata to the Chordata as Subphylum Calcichordata, will now be discussed. This reallocation is less radical than at first appears, since zoologists agree that echinoderms and chordates are related. The Hemichordata are here regarded as a phylum separate from, though related to, the Chordata, following Barrington (1965) and Hyman (1959).

The zoological argument relating echinoderms and chordates has three aspects. The first links echinoderms and hemichordates, the second links hemichordates and chordates, and the third links echinoderms and chordates directly.

The aspect of the argument linking echinoderms and hemichordates can be stated as follows:

1. Both groups have radial cleavage. 2. Both sometimes have similar larvae. 3. In both, the blastopore becomes the larval anus. 4. Both are tricoelomatous. 5. In both, the protocoele develops an opening to the exterior on the left side of the larva. 6. In both, a pulsatile vesicle (heart of hemichordates, madreporic vesicle of echinoderms) arises in close association with the protocoele (Narasimhamurti 1931 : 484, and earlier authors). The argument relating hemichordates and echinoderms is well summarised by Hyman (1959 : 197). A most elaborate series of echinoderm, hemichordate homologies was proposed by Gemmill (1914 : 277).

The aspect of the argument linking hemichordates and chordates depends mainly on the presence of gill slits in both groups (Hyman 1959 : 201). In addition, both can have a collagen-rich mesodermal skeleton, are deuterostomatous and have radial cleavage.

The third aspect of the argument, which links echinoderms and chordates directly, depends on the presence in both groups of radial cleavage, a mesodermal skeleton and deuterostomy, and the possible broad homology of water vascular and hypophyseal systems (Goodrich 1917).

The relationship between Stylophora and echinoderms, though less close than that with the chordates, is not in doubt. Stylophora, like all echinoderms, have a skeleton in which each plate is a single crystal of calcite. In addition, anterior and posterior coeloms of Stylophora may correspond to left and right somatocoels in echinoderms. Further, the Stylophora have a particular relationship with stalked echinoderms (Crinozoa, Matsumoto 1929) since: 1. In both groups there is a stem. 2. Both groups have a chambered organ and peduncular nerve in the stem, an aboral nerve centre oral (anterior) to it and nerves radiating from the aboral nerve centre to the theca. 3. Both groups have the mouth at the end of the theca farthest from the stem. 4. Among Crinozoa, crinoids at least are typically attached by the distal end of the stem. The abrupt end of the stem of Stylophora strongly suggests fracture and may indicate that a larval stylophoran attached by a hold-fast at the end of the stem, from which it subsequently broke away. 5. The vestibule of crinoids may correspond to the buccal cavity of Stylophora. 6. The broad lumen of the anterior stem of Stylophora compares with a similar broad proximal lumen in solute "carpoids", many primitive crinoids, and many eocrinoids and rhombiferan cystoids. The Stylophora differed from echinoderms most importantly by having branchial slits and no obvious water vascular system.

Crinozoa may possibly have arisen from Stylophora by the loss of branchial slits, rather than the converse. The same line of speculation suggests that Stylophora may have derived directly from Hemichordata.

Turning now to the chordate affinities of the Stylophora, of the forms here studied the Mitrocystitidae, in particular, in many ways resemble tunicate tadpoles. Thus: 1. Both are clearly divided into a body (theca) and a postanal tail (stem). 2. Both have a dorsal nerve cord resting directly on a notochord, the latter confined to the stem or tail. 3. Mitrocystitidae and appendicularian tadpoles (Martini 1909) have paired segmental ganglia in the stem or tail. 4. The brain of Mitrocystitidae had hypophyseal, optic and medullary parts which can also be recognised in tunicate tadpoles. 5. Both Mitrocystitidae and tunicate tadpoles have paired atria. 6. Both Mitrocystitidae and tunicate tadpoles have the rectum opening into the left atrium.

It should be emphasized that tunicate tadpoles resemble mitrates rather than cornutes in the paired atria and gill slits, the rectum opening into the left atrium and the subdivisions of the brain. A mitrocystitid, in fact, could be briefly described as a giant, calcite-plated tunicate tadpole. Pending further study, it is uncertain how far this description would also apply to a lagynocystid mitrate. If, as argued below, the extant chordate subphyla have risen only once from the Stylophora, then there are arguments which suggest that the Mitrocystitidae rather than Lagynocystidae were their point of origin.

Mitrocystitidae most differed from tunicate tadpoles, apart from size, in the abruptly ending stem with its posterior portion adapted to vertical flexion, the calcite skeleton and the blood system of the stem. Further, larval Mitrocystitidae, like Stylophorans in general, may have been anchored for a time by the posterior end of the stem. Tunicate larvae, on the other hand, attach by adhesive papillae, at the anterior end of the body, which may possibly be homologous with the cement glands of many fish and amphibians.

Relationship between Cephalochordata and Mitrocystitidae is indicated by the following points: 1. Both groups have a dorsal nerve cord and notochord, and segmentally repeated muscle blocks in a postanal tail. 2. Both groups have internal gill slits, with, probably in both, the left ones appearing before the right ones in ontogeny. 3. The left-facing mouth of larval amphioxus can be compared with that of mitrocystitids. Relationships of cephalochordates with mitrates more than with cornutes is suggested by the paired, internal gill slits, with the left ones appearing first in ontogeny. Relationship with primitive mitrocystitids rather than lagynocystids or advanced mitrocystitids is particularly indicated by the left-facing mouth, for, of all known Stylophora, *Chinianocarpos thorali* has the most left-facing mouth, while lagynocystids have the mouth facing right.

Cephalochordates differ most obviously from mitrates in that: 1. They lack a calcite skeleton. 2. The tail is entirely adapted for lateral flexion and does not end abruptly. 3. The longitudinal caudal blood vessels are ventral to the notochord. 4. Myotomes, notochord and dorsal nerve cord extend to the front end of the animal. 5. Segmental (dorsal root) ganglia are lacking and ventral spinal roots exist. 6. There is no brain. 7. The anus, though facing left, is external. 8. Anterior, larval adhesive organs, which were presumably lacking in mitrates if the larvae attached by the stem, have been reported in *Amphioxus* (van Wijhe 1925).

Mitrocystitidae resemble Agnatha in the following ways: 1. In both groups the dorsal nerve cord is dorsal to, and rests on, the notochord and gives rise to paired segmental ganglia (dorsal root ganglia of agnathans). 2. Both groups have segmented muscle blocks in the postanal stem or tail. 3. In both groups the brain lies at the anterior end of the notochord and can be divided into medullary, optic, hypophyseal and olfactory portions. 4. In both groups the cranial nerves include olfactory, lateralis, optic and trigeminal complexes. In both the trigeminal complex has trigemino-profundus ganglia and probably mandibular and maxillary branches. 5. Both groups have paired gill slits.

Paired gill slits and the subdivisions of the brain and the cranial nerves connect the agnathans with the mitrates rather than the cornutes, and the existence of the lateralis complex connects Agnatha with Mitrocystitidae rather than Lagynocystidae.

Among agnathans, the earliest and most primitive Heterostraci (Cyathaspididae) are particularly linked with Mitrocystitidae by having paired gill openings, small eyes, paired olfactory nerves opening into the roof of the buccal cavity, no pineal eye, and primitively marine habitat (Denison 1956, 1964; White 1958).

The most important differences between Mitrata, in particular Mitrocystitidae, and Agnatha are: 1. Agnathans, like vertebrates and other extant chordates, have a uniform tail, not ending abruptly, with the longitudinal caudal vessels ventral to the notochord. 2. If agnathans have a hard skeleton it is formed mainly of hydroxyapatite, not calcite. This is true of vertebrates in general, whose only purely calcitic parts are the otoconiae of the acustico-lateralis system. 3. The spinal nerves of agnathans have separate dorsal and ventral roots. 4. The anus of agnathans is median and external. 5. The brain of agnathans is longer and extends farther forward. 6. Agnathan eyes are often better developed. 7. The acustico-lateralis system of Agnatha includes ears.

Two features that the earliest agnathans may have lacked, although they occur in most vertebrates, were a closed circulatory system and oculo-motor muscles, for both these features are absent in myxinoids.

As regards larval attachment, recently hatched anuran tadpoles and the young larvae of many archaic living fish such as dipnoans, *Polypterus*, *Amia*, *Lepisosteus* and *Acipenser* attach themselves by cement organs near the anterior end of the body (Kerr 1919, esp. p. 178 ff.). These organs are likely to be homologous in all the cases cited and, as already mentioned, they may possibly be homologous with the adhesive papillae of tunicate tadpoles. They may also be homologous with the adhesive papillae reported in amphioxus.

The evidence for a relationship between Stylophora and the extant chordate subphyla can therefore be summarised by saying that all Stylophora had branchial slits, a stem (or tail) which is post-anal and contains segmental muscle blocks, a notochord with a brain at the front of it, and a mouth at the front end of the body. Furthermore the Mitrocystitidae, at least, resembled extant chordates in having paired branchial slits, dorsal nerve cord and segmental ganglia. The Mitrocystitidae, in particular, had a number of additional resemblances to each of the three extant subphyla, related especially to the cranial nerves and brain and to asymmetries of structure. These resemblances are most unlikely to be coincidental and clearly indicate that the extant subphyla of chordates were descended from Stylophora. It therefore seems just to transfer the Stylophora from the Echinodermata, which they resemble less markedly, to the Chordata. Since the Stylophora have resemblances to all the extant subphyla of chordates, but cannot clearly be placed in one rather than another, and since they also have features that distinguish them as a group from all the extant subphyla, it is reasonable to establish a new subphylum—the Calcichordata—to receive them.

The differences which separate all Stylophora from all extant chordates are the calcite skeleton, the adaptation of the posterior part of the stem for vertical flexion, the abrupt end of the stem which may imply attachment by the stem in the larva, and the probable presence of a longitudinal blood vessel within the notochord. These differences suggest that the other chordates have arisen from Stylophora only once. If this is the case it is the mitrates, and among mitrates the Mitrocystitidae rather than the Lagynocystidae, which were the group from which these other chordates arose, since Lagynocystidae lack the lateralis system (unlike Agnatha and fish) and have the mouth facing somewhat to the right (unlike larval amphioxus). Further, it is probably very primitive mitrocystitids which are in question since the earliest-known agnathans, which are also the earliest-known chordates other than calcichordates, are Lower Arenig in age (Bystrov 1955 : 473), while the earliest-known mitrocystitid (*Chinianocarpos thorali*) is Upper Tremadoc or Lower Arenig. This is supported by the fact that *C. thorali*, more than later mitrocystitids, has a mouth opening strongly to the left.

It should be mentioned that some peculiarities of the peduncular blood system of the Mitrocystitidae particularly studied here, i.e. the dorsal longitudinal blood vessel with interossicular vessels going up to it through the dorsal nerve canal, may have been absent from the earliest Mitrocystitidae since no dorsal longitudinal vessel exists in the Lagynocystidae. Alternatively the dorsal vascular complex may have been lost in subsequent evolution.

It is fairly certain that the Stylophoran calcite skeleton could not have directly given rise to an apatite skeleton because: 1. Calcite cannot gradually be converted to apatite, since there is nowhere in the the calcite lattice for the insertion of phosphorus ions. 2. The earliest agnathans were probably either naked or covered with loose denticles or scales, for the Arenig forms are known only as dermal denticles

(Bystrov 1955) or perhaps as fragments of scales (Ørvig 1958 : 4). Middle Ordovician agnathans, also, had skeletons consisting basically of small scales or plates, sometimes fused over the head region. Big plates superficially resembling those of Mitrocystitidae only developed later (Tarlo 1962; Denison 1964). In addition both Cephalaspidae (Westoll 1945 : 345) and primitive Osteostraci (White 1958; Denison 1964 : 459) had long, unossified larval stages. 3. Vertebrate apatite is seeded extracellularly by collagen fibrils with 650 Å repetition (e.g. Glimcher *in* Sognnaes 1960). Echinoderm calcite, and therefore presumably calcichordate calcite as well, is seeded from a tiny calcite crystal in a vacuole, intracellularly (Bevelander & Nakahara *in* Sognnaes 1960). These two processes are totally unlike.

Skeletal calcite was therefore most probably lost in the course of evolution, producing a cartilaginous skeleton resembling that which occurs in some holothurians. An apatite skeleton arose later, by seeding of apatite round the collagen fibrils. This may have happened more than once. It is interesting that the ground-mass of echinoderm calcite, like cartilage, contains abundant collagen fibrils (Randall *et al.* 1952).

The history of the evolution of other chordates from calcichordates may therefore have been somewhat as follows. In the Upper Cambrian, or at latest Tremadoc Series, a population of primitive mitrates which lived in the shallow sea and were most probably mitrocystitids resembling *Chinianocarpos*, took to swimming more and more continuously in a forward direction, like tadpoles, by flexing the anterior part of the stem from side to side.

A member of the population that did this had the rudiments of a lateral-line system, optic, olfactory and trigeminal cranial nerves, a tunicate-vertebrate ultrastructure in its visual cells, and a basically fish-like brain. It also had paired atria, paired gill openings and paired gill slits, with the left gill slits preceding the right ones in ontogeny. The rectum opened into the left atrium. The stem had an abrupt posterior end, indicating that the larva had, for a short time, been attached by the end of the stem. The stem was divided into an anterior, laterally flexing part and a posterior, vertically flexing part. In the stem were segmented muscle blocks, a notochord which ended at the front end of the stem where the brain was sited, a dorsal nerve cord, and paired ganglia located between muscle blocks. A blood vessel probably ran down the middle of the notochord. Because of its unsymmetrical front end, the animal probably rotated round its longitudinal axis as it swam, in which respect it may have differed from later mitrocystitids.

As an adaptation to swimming the skeleton grew lighter by the appearance of connective-tissue-filled spaces. These finally coalesced and calcite disappeared except, perhaps, for particles in the lateralis system (otoconiae), without which, in the absence of any skeleton heavier than water, the lateralis system would scarcely have functioned (Pumphrey 1950 : 12). Any remaining skeletal tissue was soft and collagen-rich and resembled cartilage.

At the same time the anterior part of the stem expanded at the expense of the posterior part, which was less and less used for anchorage and creeping. Finally these functions disappeared, and even larval attachment by the end of the stem was given up. The previous larval hold-fast therefore remained attached to the stem in the adult, instead of breaking away from it. There thus arose an organ closely resembling a normal, chordate tail.

As further adaptation to swimming, the sense organs and nervous system increased in complexity. The eyes moved forwards, so as to be better placed to see what the animal was swimming towards, and the brain grew longer. The lateral line system spread as a network over the whole body.

The next stage began when these soft-bodied animals again became temporarily attached as juveniles, probably while still in the yolk-feeding stage. Attachment this time took place by cement organs or adhesive papillae near the front end of the body.

One group of such animals gradually extended this period of attachment until, finally, their adults became completely non-motile, lost most of their sense organs, their tails and their brains, developed a coat of tunicin and became urochordates. The tadpole-like larvae of this group also became simplified to some extent, particularly as regards the nervous system, but retained most of the features of the ancestral juvenile stage which much resembled the ancestral adult. One ancestral feature retained by the tadpoles was rotation during swimming.

In other descendants of the animals which had adopted anterior, larval attachment, the period of attachment remained very temporary. Since the adults remained able to swim, further modification of the tail took place, i.e. the ventral spinal roots separated from the dorsal roots and the longitudinal blood vessel migrated ventrally out of the notochord, if this had not happened already. In addition, the anus became external though it still opened leftward.

From the animals so modified, evolution proceeded in two directions. In one population, perhaps as an adaptation to burrowing, the tail somites, notochord and dorsal nerve cord extended forward to the anterior end of the body with the muscle blocks outside the atria. The atria therefore united, and came to open ventrally. This population lost most of its sense organs, including the optic, olfactory and lateralis systems, and the dorsal root ganglia disappeared. In addition, the forward growth of the myotomes eliminated the brain as a rather unfortunate embryological consequence (Newth 1951 : 256). This population also developed nephridia-like excretory organs, unlike those of any other chordates. It retained the leftward-facing larval mouth, the left gill slits that preceded the right gill slits in ontogeny, and the tendency to rotate during swimming of the calcichordate ancestor. Thus arose the Cephalochordata.

From the population that produced the cephalochordates, another group of animals arose. In these, again, the attached phase of the larvae remained temporary, but the adults remained habitual swimmers in water rather than becoming burrowers. They ceased to rotate as they swam, however, which allowed the sense organs to increase greatly in complexity and accuracy. True eyes with lenses were probably evolved at this stage, and parts of the lateralis system sank into the body to function as accelerometers or ears. The bodies of these animals became more symmetrical. The anus became median. Right and left gill slits came to appear at the same time in ontogeny. Kidneys developed. Also, and perhaps more than once, apatite, seeded by collagen fibrils, produced a hard skeleton. These animals were the vertebrates. In their basic features they already existed in Arenig times.

The foregoing story is admittedly speculative, but differs from previous speculations on the origin of vertebrates in that it starts from a known beginning.

V. CONCLUSIONS

a. *Phyletic and systematic position*

A study of two members of the Order Cornuta Jaekel 1900, *Cothurnocystis elizae* Bather, and *Corthurnocystis curvata* Bather, and two members of the Order Mitrata Jaekel 1918, *Mitrocystella incipiens* (Barrande) *miloni* Chauvel and *Mitrocystites mitra* Barrande, reveals a basically similar anatomy in all. This justifies the placing of Cornuta and Mitrata in a larger group, the Stylophora Gill & Caster 1960, here regarded as a class. It is fairly certain that the Mitrata evolved from the Cornuta, rather than the converse.

The Class Stylophora is more closely allied to extant chordate subphyla than to any echinoderms, and is better placed in the Phylum Chordata than in the Phylum Echinodermata. Since it cannot be allocated to any of the extant chordate subphyla, and has features which distinguish it from these subphyla collectively, it is necessary to establish a Subphylum Calcichordata (Jefferies 1967) to receive the Class Stylophora.

With Gislén (1930), the Calcichordata are here regarded as ancestral to the other subphyla of Chordata. An Upper Cambrian mitrocystitid probably evolved into a soft-bodied, free-swimming form which gave up larval attachment by the end of the stem. This free-swimming form later took to larval attachment by cement organs near the front of the body, and by various modifications gave rise first to the Urochordata and then in turn to the Cephalochordata and Craniata.

b. *Thecal openings*

A large mouth at the anterior end of the theca is present in all four forms studied. In adult *Mitrocystella incipiens miloni* and, to a greater extent, in juvenile *Mitrocystites mitra*, the mouth opened distinctly leftward. This asymmetry was even more strongly marked in the earliest-known mitrocystitid, *Chinianocarpos thorali*. It can be compared with the leftward-facing mouth of larval amphioxus.

External branchial slits, which had the mechanical structure of outlet valves, were present in *Cothurnocystis curvata* and *Cothurnocystis elizae* on the left, dorsal part of the theca. Internal gill slits were presumably present on both sides in *Mitrocystites mitra* and *Mitrocystella incipiens miloni*. They were separated from paired branchial openings by atria.

The anus in *Cothurnocystis elizae* was external and just left of the stem. The anus of *C. curvata* was also just left of the stem but was internal, opening into the most median gill slits. In *Mitrocystella incipiens miloni* and *Mitrocystites mitra* the anus was likewise internal, opening into the left atrium as in a living tunicate tadpole.

The lateral line was developed just to the right of the stem in *M. mitra* and *M. i. miloni*.

Other thecal openings in *M. mitra* were the openings bringing the optic nerves (n_3) on to the dorsal surface and the lateral pores bringing nerves n_4 and n_5 on to the dorsal surface.

In *M. i. miloni* the optic nerves n_3 were vestigial, and nerves n_4 and n_5 did not open on the dorsal surface.

c. *Thecal chambers*

The theca of *C. elizae* was divided into buccal cavity, pharynx and anterior and posterior coeloms. These probably also all existed in *C. curvata*, though the separate existence of pharynx and anterior coelom cannot be demonstrated directly in that species.

The theca of *M. i. miloni* and *M. mitra* was divided into buccal cavity, left pharyngeal chamber, that corresponds to the pharynx of cornutes, right pharyngeal chamber, anterior and posterior coeloms and right and left atria.

The form of the right pharyngeal chamber of the two mitrates studied shows that it must have arisen in ontogeny as an outpouching from the left pharyngeal chamber, which implies that right gill slits probably appeared later in ontogeny than left gill slits, as they do in the ontogeny of amphioxus.

The form of the posterior coelom of the two mitrates studied suggests that it arose as an outpouching from the left pharyngeal chamber. Its presumed mode of origin is comparable with that of a tunicate epicardium.

The oesophagus of *M. i. miloni* probably opened into the left pharyngeal chamber near the median line of the theca.

d. *The stem*

The stem of Calcichordata is interpreted by analogy with the stem of a living crinoid. Both are compared with the tail of a living chordate, with the following suggested homologies: chambered organ = notochord, peduncular nerve = dorsal nerve cord, haemal strand broadly = caudal vessels, aboral nerve centre = brain, aboral nerves to the theca broadly = cranial nerves. In all known Calcichordata the stem has an anterior part that flexed mainly to right or left, a posterior part that flexed mainly in a vertical plane, and a medial part that included a massive element (dorsal styloid in mitrates, ventral stylocone in cornutes). A massive element of this sort must, however, have been lacking in the hypothetical transitional form between cornutes and mitrates.

The posterior stem of cornutes was fundamentally adapted for flexing upwards, and so consists of imbricating dorsal plates and massive ventral ossicles. The posterior stem of mitrates was fundamentally adapted for flexing downwards, so it consists of imbricating ventral plates and massive dorsal ossicles.

The posterior stem of the two cornutes particularly studied reveals direct evidence of segmented muscle blocks, notochord (= chambered organ) and, probably, paired segmental blood vessels. The posterior stem of the two mitrates studied reveals evidence of dorsal and ventral segmental muscle blocks, notochord, dorsal nerve cord and paired segmental ganglia connected to the dorsal nerve cord and located between muscle blocks. There was probably also a vessel, running down the middle of the notochord, that sent off vessels laterally and dorsally to the muscle blocks, and there was probably a dorsal, longitudinal vessel.

Prof. Ubaghs' comparison between the stem of cornutes and mitrates and the arm of an asteroid must be mistaken since: 1. The plates here held to be dorsal in cornutes and ventral in mitrates, which Ubaghs regards as homologous and representing cover plates, are ill adapted to open outwards, particularly in the cornute *Cothurnocystis curvata* and the mitrate *Mitrocystella barrandei*. 2. If the mutual orientation of cornutes and mitrates here adopted is correct, then Prof. Ubaghs must be mistaken, because in neither group can the impressions on the internal surfaces of the ossicles (ventral in cornutes, dorsal in mitrates) represent the *outside* of a water vascular system. This mutual orientation depends mainly on the disposition of the thecal chambers.

e. *The brain and cranial nerves*

The brain of the two cornutes studied is at the anterior (proximal) end of the stem, like the aboral nerve centre of crinoids. It can be shown to give rise anteriorly to paired median-line nerves, which go under the rectum, and to paired pyriform bodies. The median-line nerves may correspond to the nerves n_0 of mitrates. The pyriform bodies correspond to the like-named bodies of mitrates. Two upward protrusions of the anterior coelom into the pharynx of *C. elizae* may have carried the peripheral ends of optic nerves (n_3 of mitrates) near the dorsal side of the theca. In addition to these features, much more of the cranial nerve complex of mitrates may have been represented by homologous nerves in cornutes but if so, these did not touch the skeleton.

The brain and cranial nerves of the two mitrates studied were extremely complex and fundamentally fish-like in plan. The brain had an anterior, a medial and a posterior part, equivalent respectively to telencephalon, diencephalon plus optic lobes, and medulla plus ventral mesencephalon. The medial part of the brain had an upper, optic portion, and a lower hypophyseal portion. From the posterior part of the brain, paired posterior part nerves (medullary nerves) went off. From the medial part, paired medial part nerves (optic nerves) went off. Medial and posterior part nerves probably joined on each side to form the paired palmar nerves, which must have communicated laterally with the paired pyriform bodies. They gave rise peripherally to paired nerves n_1 to n_5, which, with the palmar nerves, constitute the palmate complexes.

Other important features of the cranial nerves of the mitrates studied were the peripheral canals of *M. i. miloni*, the corresponding peripheral grooves of *M. mitra*, the paired olfactory openings to the buccal cavity, the lateral-line ganglion which communicated with the lateral line and was situated just behind the right pyriform body, and paired nerves n_0, near the median line.

By analogy with cephalaspids, which are here interpreted according to Lindström (1949), nerves n_1 of the palmate complexes probably represent the mandibular trigeminal nerves of agnathans; nerves n_2 represent the maxillary trigeminal nerves of agnathans; nerves n_3 represent the optic nerves; nerves n_4 and n_5, which innervate the probably sensory peripheral canals or grooves, may possibly represent the sensory field nerves of cephalaspids. The pyriform bodies are probably homologous with the trigemino-profundus ganglia of agnathans. The olfactory system of *M. i. miloni* and *M. mitra* resembled that of Heterostraci and gnathostomatous fish rather than that of cephalaspids. The nerves n_0 may possibly represent the hyomandibular branches of the facial nerves of agnathans.

The optic system of *M. i. miloni* was in all its parts degenerate compared with that of *M. mitra*, whose optic nerves (n_3) ended peripherally in little bulbs external to the skeleton, i.e. eyes.

f. *Posture and habits*

The two cornutes studied habitually lay on the ventral side, as suggested by previous authors. They probably pulled themselves backwards by sideways movements of the stem. *C. elizae* was a deposit feeder and *C. curvata* a suspension feeder.

The two mitrates studied also lay habitually on the ventral side, which most previous authors have regarded as uppermost. They probably pulled themselves backwards by ventral flexing of the stem, and may also have been able to swim forwards by lateral flexing of the stem.

g. *Definition of Subphylum Calcichordata* (Jefferies 1967)
= *Class Stylophora* (Gill & Caster 1960)

Primitive chordates with a skeleton made of calcite plates, each of which is a single crystal. Animal clearly divided into a stem and a theca (tail and body). Stem ending abruptly, with a vertically flexing posterior part, a laterally flexing anterior part and an abrupt posterior end, perhaps indicating larval attachment by the stem. Gill slits present, either internal or external, either confined to the left side, or paired. Mouth at anterior end of theca. Buccal cavity, pharynx, anterior and posterior coeloms, and sometimes other chambers, recognisable in the theca. Brain at anterior end of stem, giving rise to paired pyriform ganglia and sometimes a complex of cranial nerves anteriorly. Stem with notochord and muscle blocks, and sometimes demonstrably provided with dorsal nerve cord and segmental ganglia.

Stratigraphical range: Middle Cambrian to Devonian.

Formal definitions of the orders Cornuta and Mitrata would at present be premature.

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EXPLANATION OF PLATES

All illustrated specimens of *Cothurnocystis elizae* and *C. curvata* are from the Starfish Bed, Ashgill Series, Girvan, Scotland. All *Mitrocystella incipiens miloni* are from the Schists à Calymènes (Llandeilo Series), Grand Champ de Traveusot, Traveusot, Ille-et-Vilaine, France. The horizons and localities of *Mitrocystella incipiens incipiens*, *M. barrandei* and *Mitrocystites mitra* are given for each specimen.

Standard plate and ventral spike notations e.g. M_{1LD}, D_{OL}, S_{1L} are not explained in the captions.

A = Sedgwick Museum, E = British Museum (Natural History), GSM = Geological Survey Museum, IG = Institut de Géologie, Rennes, MCZ = Museum of Comparative Zoology, Harvard, NM = Narodní Museum, Prague.

PLATE 1

Cothurnocystis elizae

FIG. 1. E 23137. Latex cast showing interior of gill slits. au = anterior u-plate ; f = flap; pu = posterior u-plate ; rp = reniform process.

FIGS. 2, 3. E 23157. Latex casts of dorsal and ventral surfaces of juvenile. an = anus ; cp = crestal plate ; stc = stylocone ; str = strut.

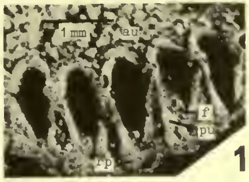
FIGS. 4, 5, 6. E 23394. Ventral, dorsal and oblique lateral aspects of latex casts. Note variation in form of ventral stem ossicles in fig. 4, anterior points on ventral spikes in fig. 6. lap = left appendage ; loap = left oral appendage ; rbcr = ridge posterior to buccal cavity on right ; roap = right oral appendage ; stc = stylocone ; vo = ventral ossicle without boss ; vob = ventral ossicle with boss.

FIG. 7. E 28657. Latex cast. Dorsal aspect. Note contrast between plates of dorsal integument in the " foot " region generally, in the region just posterior to the branchial slits and in the " ankle " region. adp = antero-dorsal process ; dp = dorsal plate ; f = flap ; rbcr = ridge posterior to buccal cavity on right.

FIG. 8. E 23179. Latex cast. Dorsal aspect showing branchial slits. The flaps indicated f have been slightly displaced after death relative to the posterior u-plate.

FIG. 9. E 23352. Latex cast. Anterior aspect of internal surface of posterior marginals cf. Text-fig. 3E. 2 = point on pharyngo-visceral line (pvl), cf. Text-fig. 4d. pco = posterior coelom.

FIG. 10. E 23705. Latex cast. Dorsal surface. Large individual with circular plates in the dorsal integument of the " ankle " as well as " foot " region. an = anus ; if = imbrication flap of ventral plate of anterior stem.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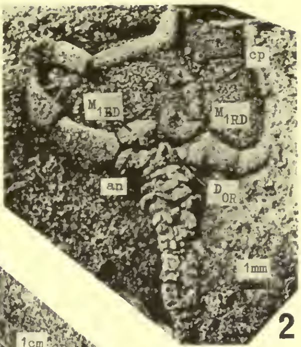
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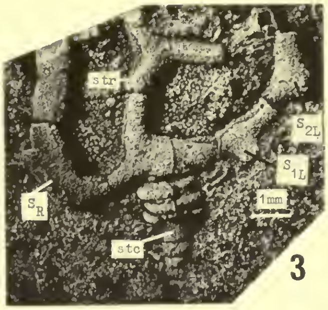
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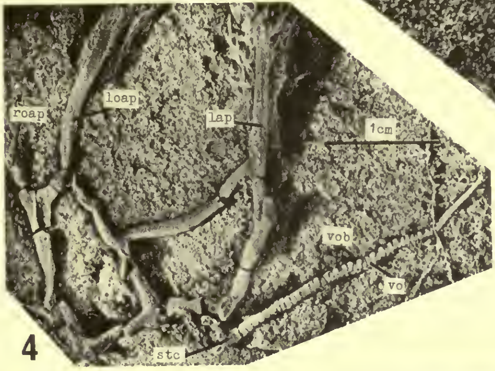
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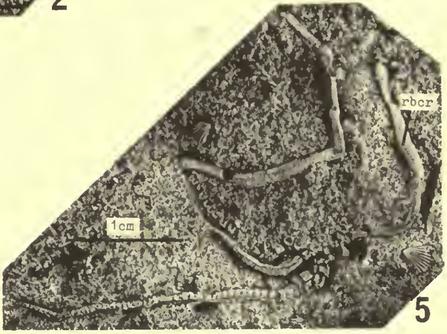

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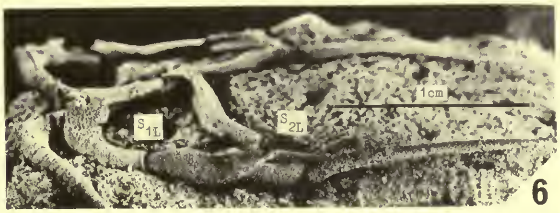

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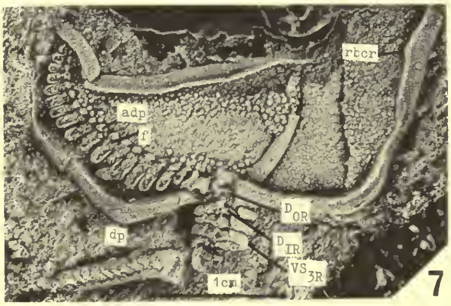
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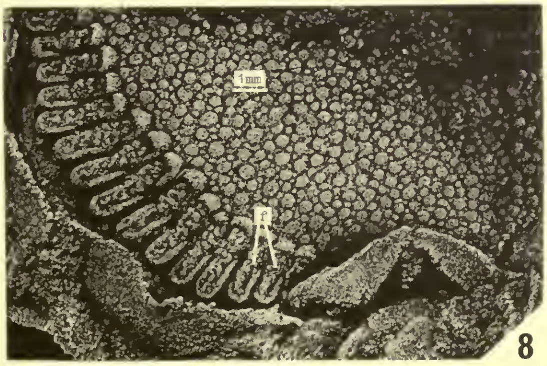

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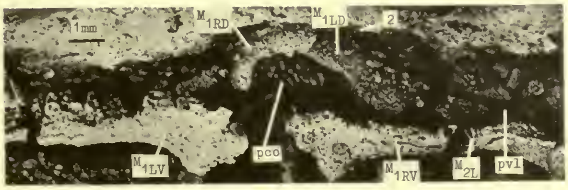
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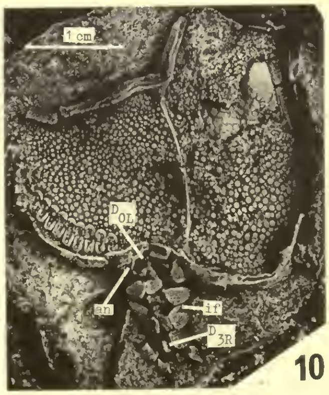
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PLATE 2

Cothurnocystis elizae

Figs. 1, 5, 6, 7. E 28644. Natural mould, ventral aspect. pco = posterior coelom ; rbcr = ridge behind buccal cavity on right ; rg = rectal groove. 5, oblique right aspect, ventral side upwards. 6, cast of cerebral basin. 7, posterior coelom, posterior aspect. 4/5, 5, points on pharyngo-visceral line, cf. Text-fig. 4c. mlnl = left median line nerve ; nmln = notch for median-line nerves ; pbl = left pyriform body ; pbr = right pyriform body ; pco = posterior coelom ; pvl = pharyngo-visceral line ; rbcr = ridge (on skeleton) delimiting buccal cavity posteriorly on right ; rg = rectal groove (on skeleton) ; sp = striations of pharynx.

Fig. 2. E 28667. Natural mould. Postero-ventral aspect, ventral side upwards. Cf. Text-fig. 4d. 1, 1/2, 3, 3/4, 4, 4/5—points on pharyngo-visceral line. For other letters see explanation to fig. 1, etc.

Fig. 3. E 28660. Latex cast, dorsal aspect. acp = area of circular plates in anterior, left, ventral integument ; rbcr = ridge behind buccal cavity on right.

Fig. 4. E 23723. Latex cast. Ventral aspect. Juvenile specimen ; spikes all ill-developed except S_R which is lateral instead of ventral ; articulation at base of right oral appendage (roap) visible. mo = mouth.

Fig. 8. E 28639. Latex cast. Antero-dorsal aspect of inside of theca just anterior to stem. Cf. Text-fig. 3b. gmln = groove for median-line nerve ; hf = horizontal flange of M_{1R+LV}; nmln = notch for median-line nerves ; pbd = depression for pyriform body ; rg = rectal groove ; rpc = ridge delimiting posterior coelom.

Fig. 9. E 23705. Latex cast. Dorsal aspect of ventral ossicles of posterior stem. Cf. Text-fig. 6. dp = dorsal plate (fragment) ; fdp = facet for dorsal plate ; lpt = lateral pit ; mg = median groove ; tg = transverse groove.

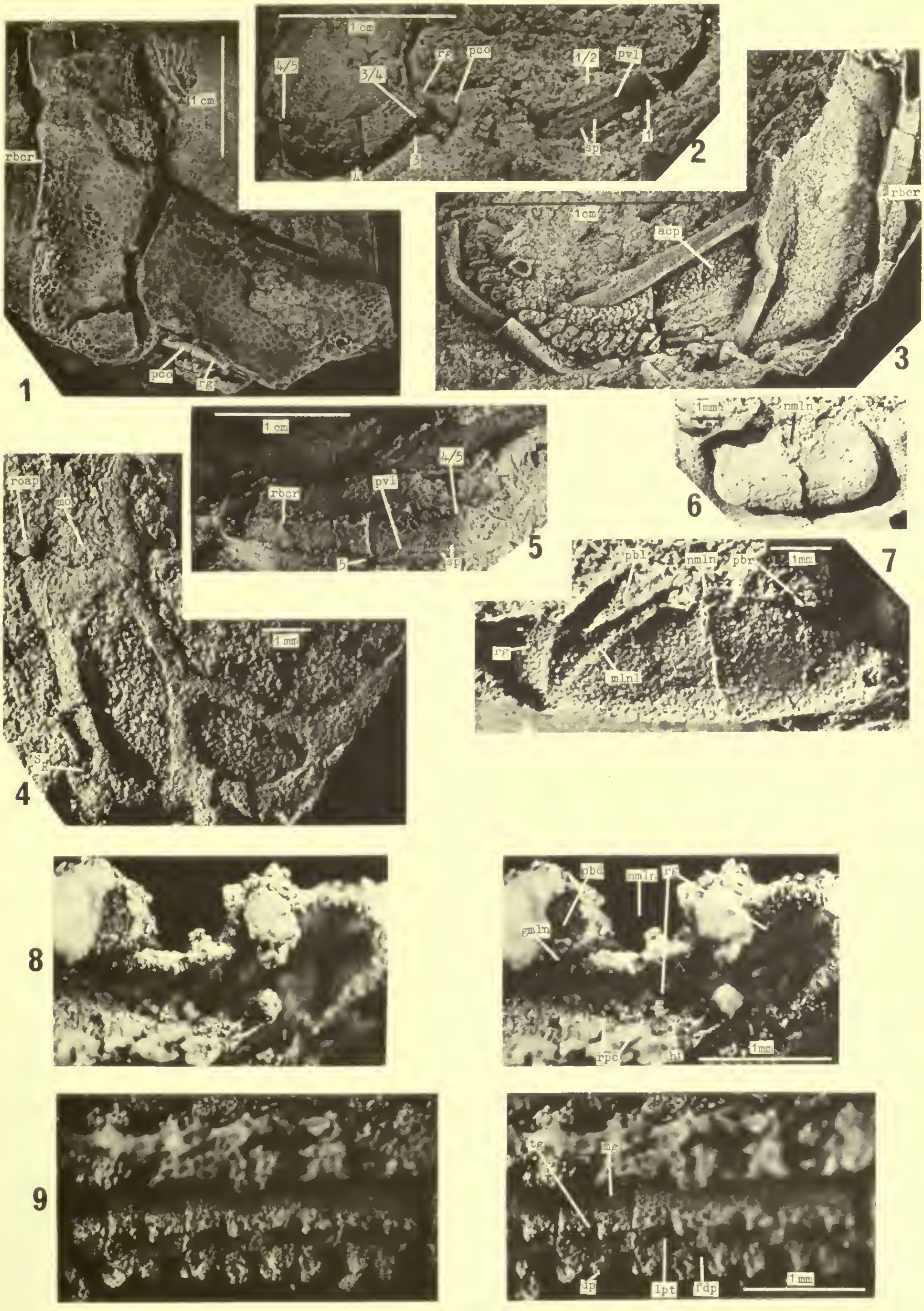
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PLATE 3

Cothurnocystis elizae

FIG. 1. E 28639. Latex cast. Dorsal aspect to show right and left internal ridges delimiting the posterior margin of the buccal cavity (rbcl, rbcr). str = strut.

Cothurnocystis curvata

FIGS. 2, 3, 6. E 28652. 2, dorsal aspect. 3, ventral aspect. 6, anterior aspect. Cf. Text-figs. 7a, b, c. bs = branchial slit ; lap = left appendage ; mo = mouth ; pco = posterior coelom ; rbcl, rbcr = ridges delimiting buccal cavity on left and right sides ; str = strut.

FIG. 4. E 28662. Dental rubber cast. Ventral aspect of branchial complex. Cf. Text-fig. 9. aep = anterior excavate process ; arc = arcuate canal, formed from apposed arcuate grooves ; pep = posterior excavate process ; vg = ventral groove ; y = point where neighbouring chevrons touch each other, ventral to the arcuate canal.

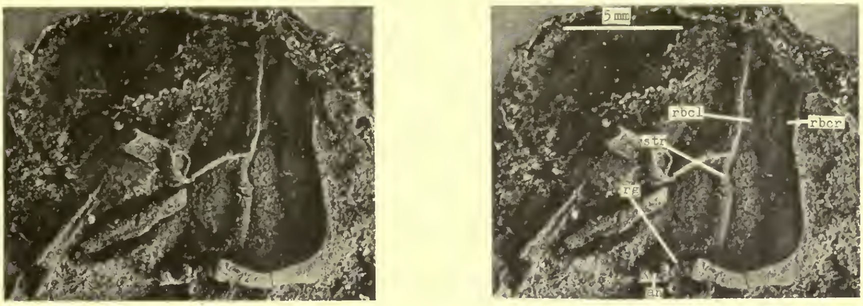
FIG. 5. E 28652. Latex cast. Same specimen as figs. 2, 3, 6. Dorsal aspect of posterior coelom, the roof of which is incomplete. Cf. Text-fig. 10a.

FIG. 7. E 28551. Latex cast. Ventral aspect. Specimen shows right and left appendages (rap, lap) and supernumary ventral spike (S_{3R}).

FIG. 8. E 23168. Latex cast. Posterior aspect. Cf. Text-fig. 11c.

FIG. 9. GSM 60839. Natural mould. Note distal rectal canal (drc) leaving rectal groove (rg) and opening near the most median branchial slits. bs = branchial slit ; pco = posterior coelom. The branchial skeleton and dorsal integument are represented by moulds of their external surfaces.

FIG. 10. E 28650. Latex cast. Dorsal aspect of anterior stem and region in front of it to show absence of external anus. bs = branchial slit.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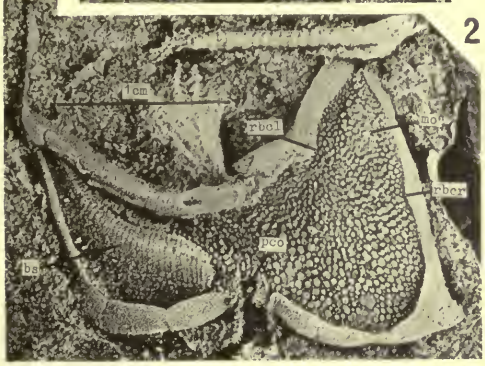
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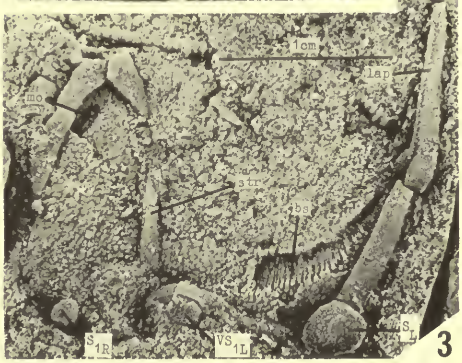
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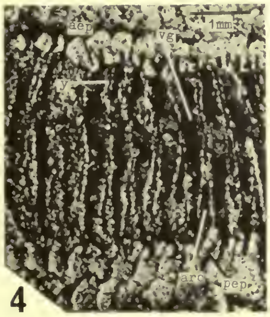
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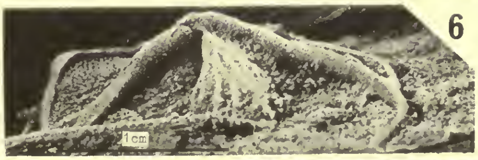
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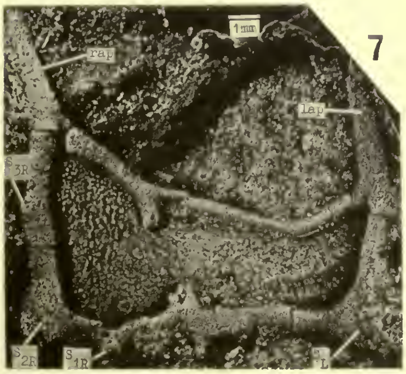
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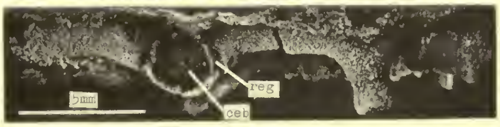
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PLATE 4

Cothurnocystis curvata

Figs. 1, 4. E 28661. Dental rubber cast of posterior stem. 1, right aspect ; 4, dorsal aspect. Cf. Text-fig. 12. admp = admedian process ; afc = anterior facet ; dp = dorsal plate ; mg = median groove ; tb = transverse buttress ; tg = transverse groove. Arrows point towards theca.

Figs. 2. 3. E 28656. Natural mould of region of buccal cavity, ventral side downwards, to show sculpture on internal mould of theca. 2, left aspect. 3, right aspect. bc = buccal cavity ; liaf = lower integument attachment facet ; uiaf = upper integument attachment facet.

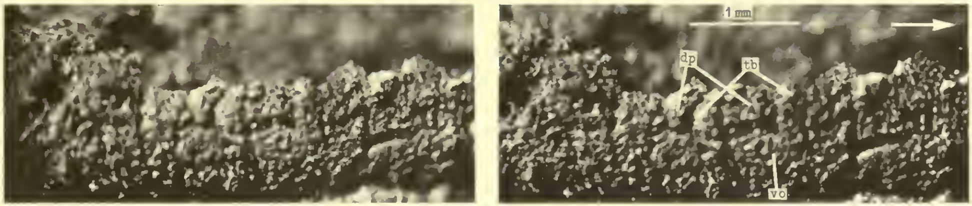
Figs. 5, 6. E 28572. Natural mould of inside of theca, to show superficial internal sculpture. Ventral side upwards. Cf. Text-fig. 10. 5, posterior aspect. 6, left aspect. ph = pharynx ; liaf = upper integument attachment facet ; uiaf = lower integument attachment facet.

Fig. 7. E 28893. Natural mould of internal cast, anterior aspect. Cf. Text-fig. 10a. liaf = lower integument attachment facet ; ph = pharynx ; uiaf = upper integument attachment facet ; str = strut.

Mitrocystella incipiens miloni

Fig. 8. IG 90. Latex cast. Ventral surface. or = oral plate ; tr = transverse ridge. M_{1RV}, first right ventral marginal.

Figs. 9, 10. *M. i. miloni*. E 23665. Dental rubber cast. 9, posterior aspect. 10, right aspect. ng = narrow groove (lateral line).



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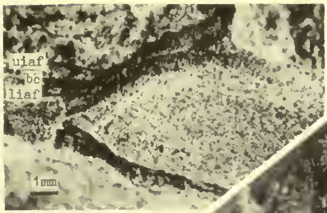
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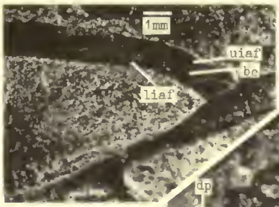
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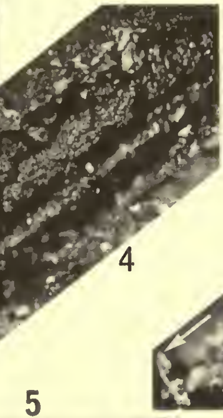

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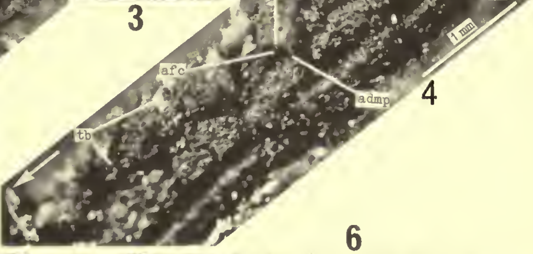
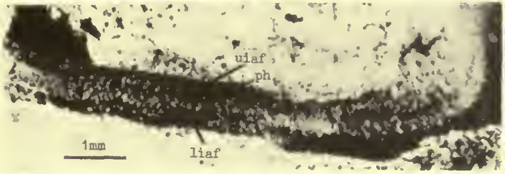
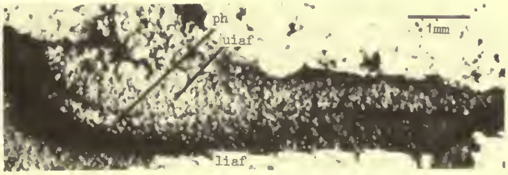

tg
mg
dp
1mm
afc
admp
tb

4

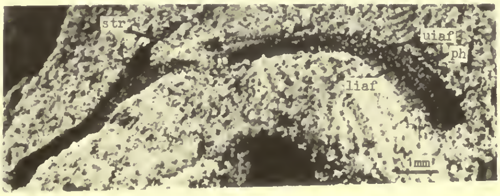
5


uiaf
ph
1mm
liaf

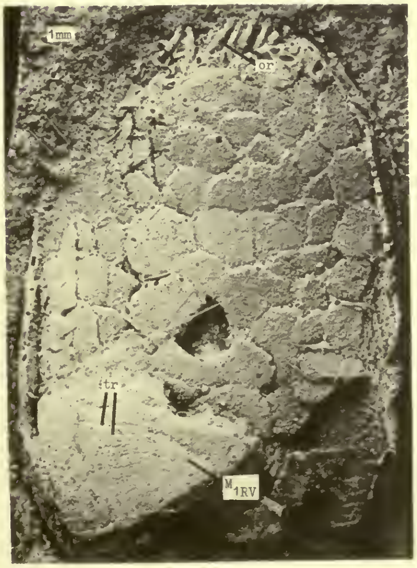
6


ph
uiaf
1mm
liaf

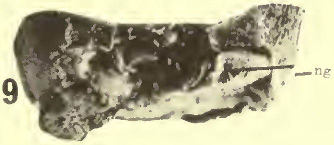
7


str
uiaf
ph
liaf
1mm

8


1mm
or
tr
M_{1RV}

9



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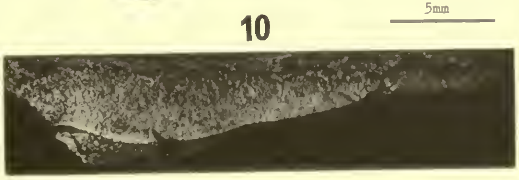


PLATE 5

Mitrocystella incipiens miloni

FIGS. 1, 4. IG 18. Natural mould. 1, dorsal, 4, posterior aspect. gpco = groove limiting posterior coelom ; grp = groove limiting right pharyngeal chamber ; la = left atrium ; lph = left pharyngeal chamber ; n_2 = nerve n_2 of palmar complex ; pal = base of palmar nerve ; pco = posterior coelom ; rb = rectal bridge ; rr = rectal ridge.

FIG. 2. IG 30. Latex cast of dorsal surface. Note calcite cleavage cracks (ccc).

FIGS. 3, 6. IG 110. Natural mould. 3, left posterior part of theca, dorsal aspect. 6, right posterior part of theca, postero-ventral aspect, dorsal side upwards. af = anterior furcation of palmate complex ; csb = carrot-shaped body (lateral-line ganglion) ; e = vestigial eye ; n_{1-5} = nerves of palmate complex ; pal = palmar nerve ; pb = pyriform body ; pc = peripheral canal ; pf = posterior furcation of palmate complex.

FIG. 5. IG 348. Latex cast of posterior stem. Left aspect. ia = interossicular articulation ; do = dorsal ossicle ; vp = ventral plate ; x = point where ventral plate overlaps dorsal ossicle.

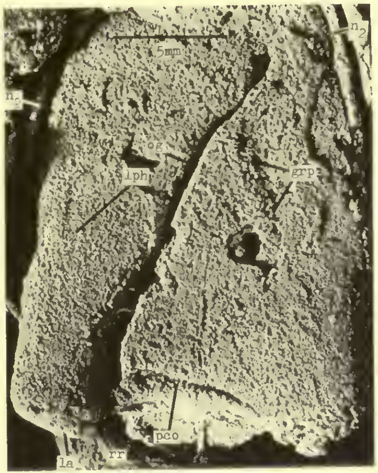
FIG. 7. E 28887. Natural mould. Dorsal aspect of anterior part to show buccal cavity (bc) as it appears before dissection cf. fig. 9. n_2 = nerve of palmar complex ; og = oblique groove ; olo = olfactory opening.

FIG. 8. IG 70. Natural mould. The surface shown is a cast of the inside of the external layer of plate M_{1RV}. af = anterior furcation of palmate complex ; csb = broken-off carrot-shaped body (lateral-line ganglion) ; n_{1-5} = nerves of palmate complex ; pal = palmar nerve ; pf = posterior furcation of palmate complex ; pb = pyriform body ; tol = cast of thickening of outer layer of calcite.

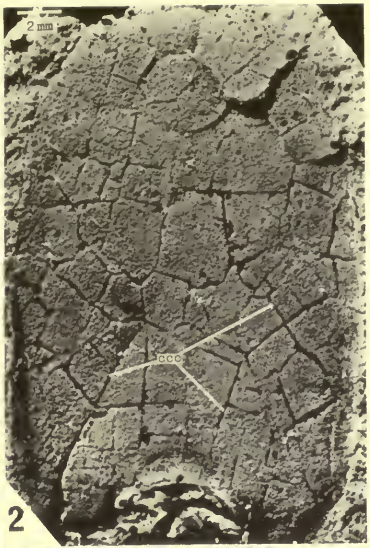
FIG. 9. E 23664. Natural mould. Dorsal aspect of anterior part with buccal cavity partly dissected out. Cf. fig. 7. For legend see fig. 7.

Fig. 10. E 23664. Dental rubber cast, representing dorsal posterior skeleton of theca, ventral aspect. To show nature of separation (llpc) between posterior coelom (pco) and left pharyngeal chamber (lph). obr = oblique ridge ; pb = cupule for pyriform body ; rpco = ridge limiting posterior coelom.

Fig. 11. IG 91. Natural internal mould, ventral aspect of right posterior part. gpco = groove limiting posterior coelom ; n_0 = nerves n_0 ; n_{1-3} = grooves representing nerves of palmate complex ; M_{1RV} = first right ventral marginal plate ; V_{PM} = posterior, median ventral plate (displaced).


5mm
n2
og
lph
grp
pco
la
rr

1



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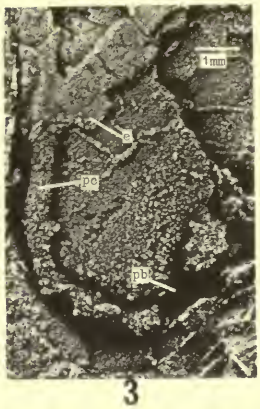

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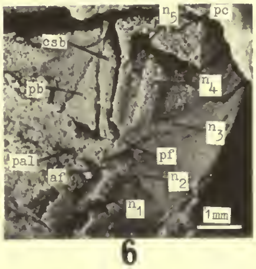
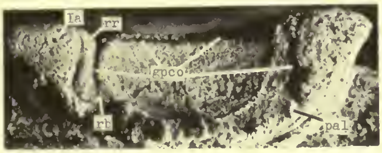
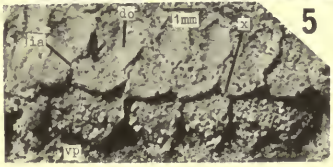

n5
pc
csb
n4
pb
n3
pal
pf
af
n2
n1
1mm

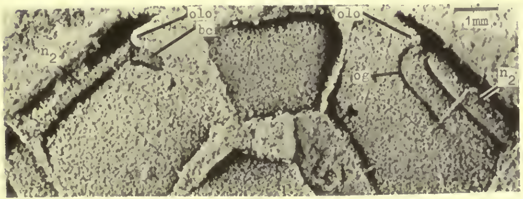
6


la
rr
gpco
rb
pal

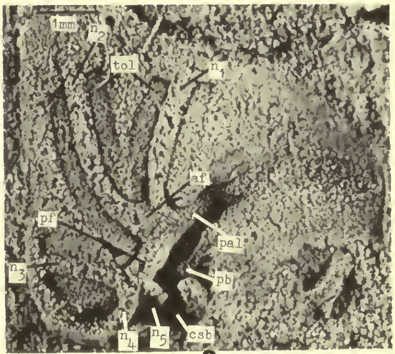
4


do
1mm
x
ia
vp

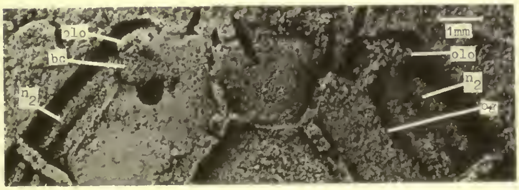
5


olo
bc
olo
1mm
n2
og
n2

7

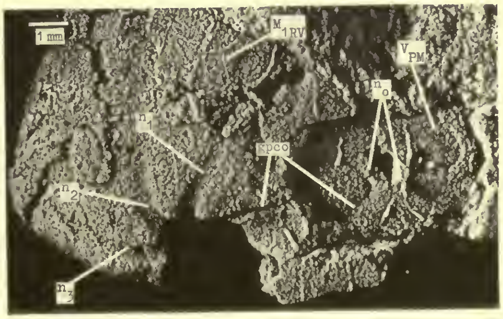

1mm
n2
tol
n1
af
pf
pal
n3
pb
n4
n5
csb

8


olo
1mm
olo
bc
n2
n2

9

11


1 mm
M 1RV
V PM
n o
n1
xpco
n2
n3

10

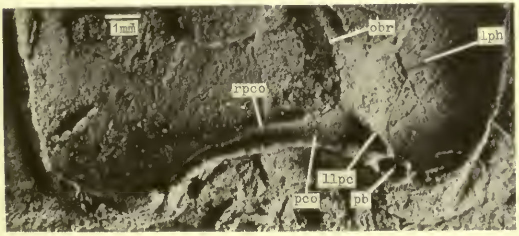

1mm
obr
lph
rpco
llpc
pco
pb

PLATE 6

Mitrocystella incipiens miloni

FIG. 1. A.4627/a. Natural internal mould, dorsal·aspect, posterior part. ap = anterior part of brain ; e = eye ; lph = left pharynx; mp = medial part of brain ; pc = peripheral canal ; pco = posterior coelom ; pp = posterior part of brain.

Mitrocystella barrandei

FIG. 2. NM Akc Kat 437/65. Šarká Beds, Osek Czechoslovakia. Natural mould of cerebral depression representing brain, antero-ventral aspect, dorsal side upwards. lmp = lower medial part of brain (enclosed in life by hypocerebral processes) ; mpf = medial part foramen ; pp = posterior part of brain ; ppn = posterior part nerve ; ump = upper medial part of brain ; w = point of division between lmp and ump.

FIG. 3, 5. E 7517. Šarká Beds, Rokycany, Czechoslovakia. Latex cast. 3, detail of stem, 5, ventral aspect. as = anterior stem ; do = dorsal ossicle ; ia = interossicular articulation ; or = oral plate ; vp = ventral plate ; x = point where ventral plate overlaps dorsal ossicle.

Mitrocystella incipiens miloni

FIG. 4. IG 3. Natural mould representing brain, antero-dorsal aspect. mp = medial part of brain ; mpf = medial part foramen ; ng = narrow groove (lateral line) ; pb = pyriform body ; pp = posterior part of brain ; ppn = posterior part nerve.

Mitrocystites mitra

FIG. 6. MCZ 565. Šarká Beds, Osek. Natural mould, dorsal aspect of posterior part. la = left atrium ; mp = medial part of brain ; n_2, n_3, n_{4+5} = nerves of palmate complex ; mp = medial part of brain ; og = oblique groove ; pp = posterior part of brain ; ra = right atrium.

M. i. miloni

FIG. 7. IG 355. Internal cast of M_{1RD}. ccc = calcite cleavage cracks ; pc = peripheral canal ; sc = short canals across $M_{1/2R}$, possibly carrying olfactory fibres.

Mitrocystites mitra

FIG. 8. NM Akc Kat 22011, 1923, 681. Hanuš Colln. 256. Šarká Beds, Šarká, Czechoslovakia. Latex cast. Same specimen as Pl. 10, fig. 4. Dorsal aspect of oral plates. hg = hmiecylindrical groove ; or = oral plates.

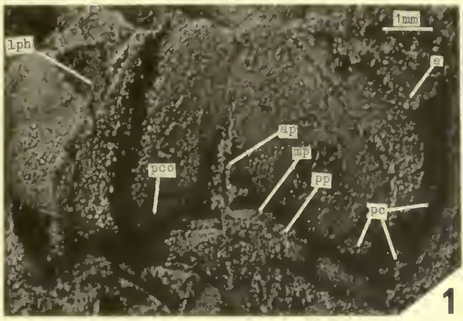
FIG. 9. NM Akc Kat. 22011/1923. Šarká Beds, Šarká. Natural mould of anterior surface of posterior stem ossicle. aig = anterior interossicular groove ; aiid = anterior inner interossicular depression ; aoid = anterior outer interossicular depression ; dlc = dorsal, longitudinal canal.

Mitrocystella incipiens miloni

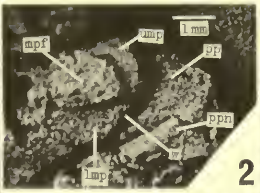
FIG. 10. IG specimen h. Natural mould of ventral side of a dorsal, posterior stem ossicle giving representation of original soft structures. dnc = dorsal nerve cord ; gap = ganglionar process ; lg = lateral ganglion ; not = notochord ; pig = posterior interossicular groove ; pogp = post ganglionar process ; z = boundary between dnc and not.

FIG. 11. IG 45. Internal cast of posterior dorsal posterior stem ossicle, right aspect. aiid = anterior, inner, interossicular depression ; aoid = anterior, outer, interossicular depression ; dlc = dorsal longitudinal canal; mg = median groove infilling (= notochord); pig = posterior interossicular groove ; piid = posterior inner interossicular depression ; poid = posterior, outer, interossicular depression.

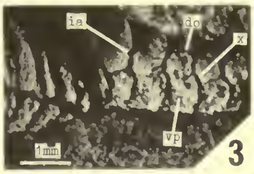
FIG. 12. A 46271 (same individual as in Pl. 6, fig. 1 and Pl. 7, fig. 3). als = anterior lumen of styloid ; dlc = dorsal longitudinal canal ; vgls = vertical groove on lumen of styloid.


lph
1mm
e
ap
mp
pp
pco
pc

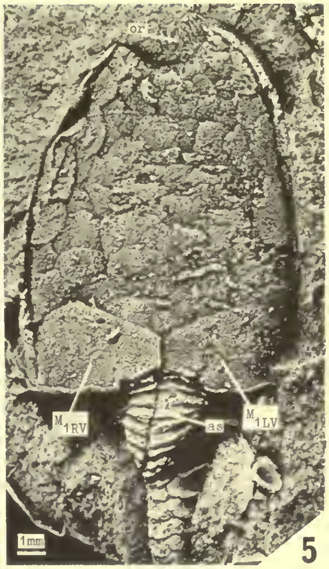
1


mpf
ump
1 mm
pp
ppn
w
lmp

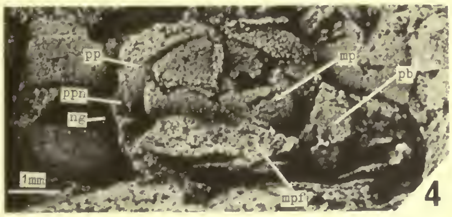
2


ia
do
x
vp
1mm

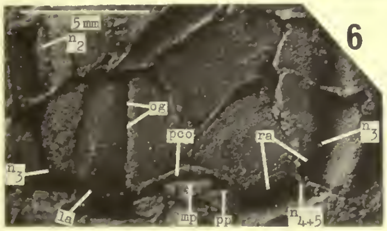
3


or
M_{1RV}
as
M_{1LV}
1mm

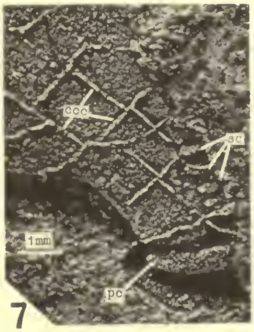
5


pp
ppn
ng
1mm
mp
pb
mpf

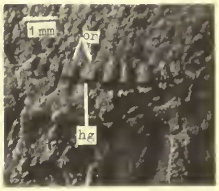
4


5 mm
n_2
og
pco
ra
n_3
n_3
la
mp
pp
n_{4+5}

6


ccc
sc
1mm
pc

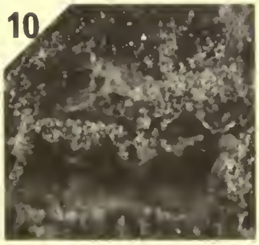
7

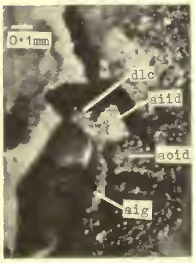


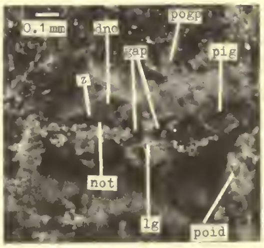
8

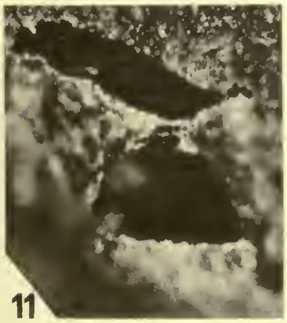
9

10




0·1mm
dlc
aiid
aoid
aig


0.1 mm
dnc
pogp
gap
pig
z
not
lg
poid



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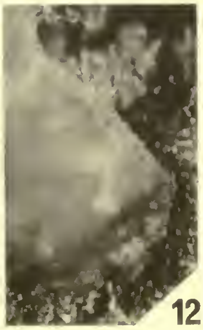

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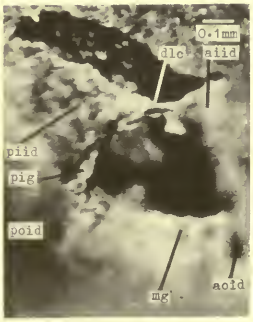

0·1mm
dlc
aiid
piid
pig
poid
mg
aoid

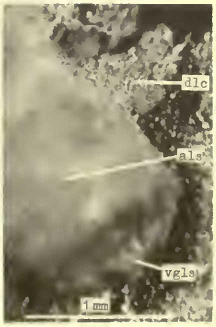

dlc
als
vgls
1 mm

PLATE 7

Mitrocystella incipiens miloni

FIG. 1. E 28889. Trace of palmar nerve (pal) on anterior face of posterior coelom.

FIG. 2. IG 48. Natural mould of ventral side of dorsal posterior stem ossicle immediately behind styloid. Theca right of picture. lga = left ganglion; rga = right ganglion; ic = interossicular canal. For other legends see Pl. 6, fig. 10.

FIG. 3. Internal natural mould of styloid. A 46271. Same specimen as Pl. 6, figs. 1, 12. ic = interossicular canal between fused ossicles of styloid; lg = lateral groove; pig = posterior interossicular groove; piid = posterior inner interossicular depression; poid = posterior outer interossicular depression.

Mitrocystites mitra

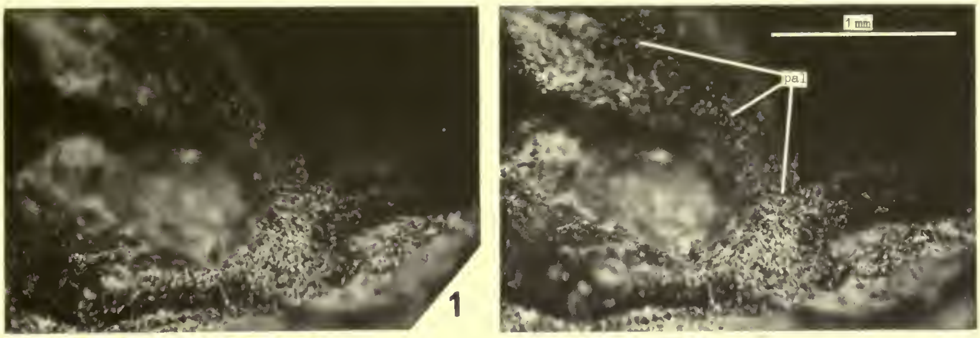
FIG. 4. Same specimen as Pl. 6, fig. 9. Internal mould of M_{2L}; on_3 = opening of n_3 on to dorsal surface; sl = excavation in skeleton for soft layer of skeleton.

Mitrocystella incipiens incipiens

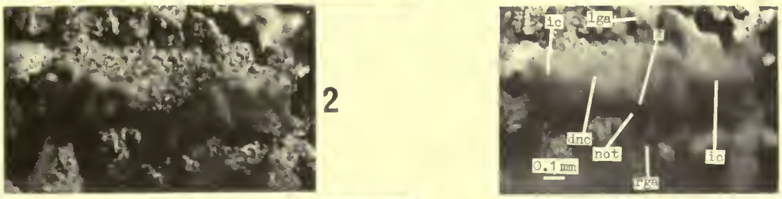
FIG. 5. MCZ 580. Šarká Beds, Svata Dobrotivá, Czechoslovakia. Internal mould of posterior stem. dlc = dorsal longitudinal canal; gmb = groove separating muscle blocks; iid = infilling of interossicular depression; not = notochord; oid = outer, interossicular depression.

Mitrocystella incipiens miloni

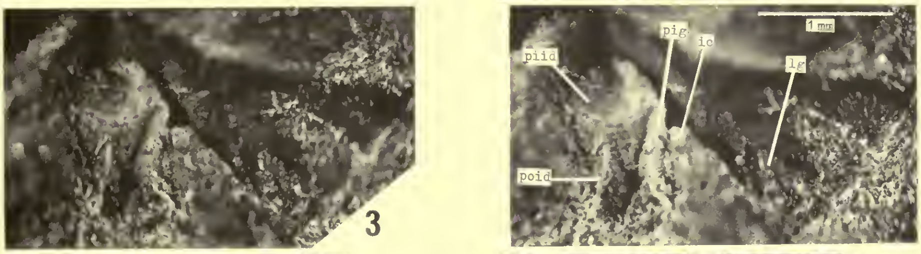
FIG. 6. IG 48. Natural internal mould, posterior part, left-dorsal aspect. og = oblique groove; sll = infilling of excavation in skeleton for reception of lateral extensions of ventral soft layer; slp = the same for posterior extensions of ventral soft layer.


1 mm
pal

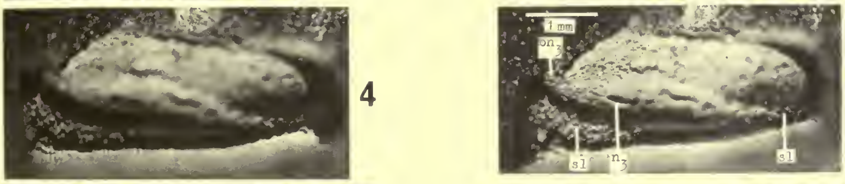
1


ic
lga
dnc
not
0.1 mm
rga
ic

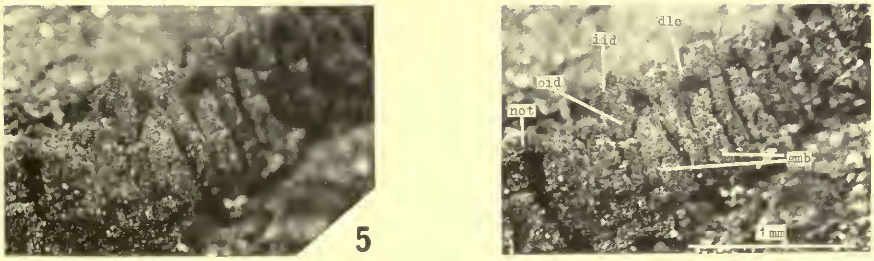
2


1 mm
piid
pig
ic
lg
poid

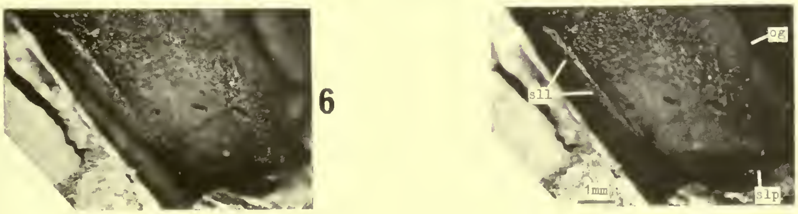
3


1 mm
on$_3$
sl
n$_3$
sl

4


dlo
iid
oid
not
gmb
1 mm

5


og
sll
1mm
slp

6

PLATE 8

Mitrocystites mitra

FIG. 1. E 16062. Šarká Beds, Osek, Czechoslovakia. Dental rubber cast, dorsal aspect. dn$_3$ = depression at end of nerve n$_3$ (optic depression) ; do = dorsal ossicle ; ia = interossicular articulation ; lp = lateral pore ; pg = peripheral groove ; on$_3$ = opening of nerve n$_3$ on to dorsal surface ; std = styloid.

FIGS. 2, 4, 6. MCZ 566. Šarká Beds, Osek. Dental rubber casts. 2, dorsal aspect of M1LV. 4, ventral aspect of posterior left, dorsal skeleton. 6, antero-ventral aspect of the same, dorsal side upwards. af = articular facet ; bo = branchial opening ; bsl = break in slope anterior to af ; gmpn = groove for medial part nerve ; hcp = hypocerebral process ; il = inner layer of skeleton ; la = left atrium ; mpf = medial part foramen ; obr = oblique ridge ; ol = outer layer of skeleton ; pb = cupule for pyriform body ; rpc = ridge delimiting posterior coelom ; sl(n$_{4+5}$) = cavity for soft layer of skeleton carrying nerves n$_4$ and n$_5$.

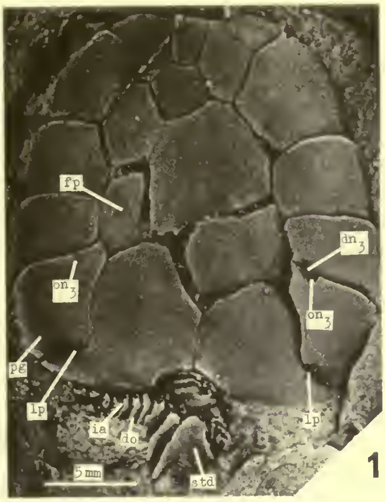
FIG. 3. NM Akc Kat 22011/1923, Inv. no. 511, Šarká Beds, Šarká. Latex cast. Ventral aspect of posterior part of theca. ng = narrow groove (lateral line) ; bo = branchial opening.

FIG. 5. NM Akc Kat 22011/1923 Hanuš Collection no. 354 +. Latex cast. Ventral aspect of dorsal skeleton. Juvenile specimen showing fenestrated calcite and leftward facing mouth. ceb = cerebral basin ; obr = oblique ridge ; olo = olfactory opening.

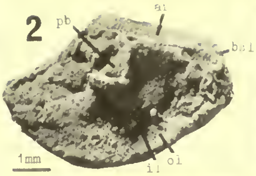
FIGS. 7, 9. E 16067. Šarká Beds, Osek. Natural mould of cerebral basin representing brain. 7, anterior aspect. 9, right aspect. ap = anterior part ; mp = medial part ; pp = posterior part ; ppn = posterior part nerve.

FIG. 8. NM Barrande Collection. Osek. Latex cast, ventral aspect. or = oral plate ; por = post oral plate.

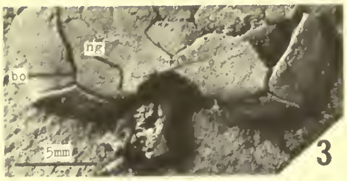
FIG. 10. MCZ. 567. Natural internal mould, dorsal aspect. The specimen has been encrusted by a branching epizoan. la = left atrium ; mb = median branch of oblique groove ; mp = medial part of brain ; n$_2$ = main trunk of nerve n$_2$, n$_{2A}$ = anterior branch of nerve n$_2$; n$_3$ = nerve n$_3$ (optic nerve) ; og = oblique groove ; olo = olfactory opening ; pp = posterior part of brain ; rr = rectal ridge ; tr = transverse ridge.


fp
dn3
on3
on3
pg
lp
lp
ia
do
std
5 mm

1


pb
ai
bsi
il
oi
1mm

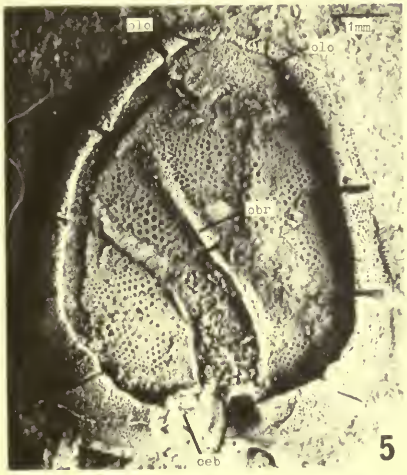
2



3

1mm
obr
sl(n4+5)
rpc
pb
la

4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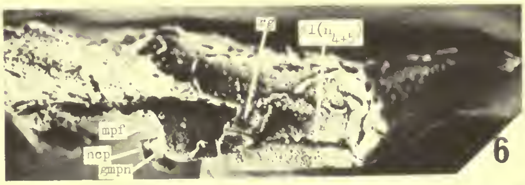
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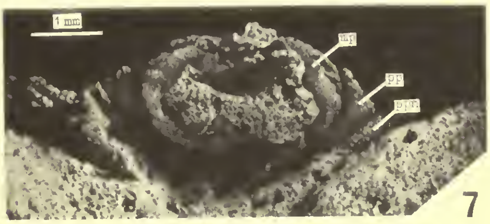
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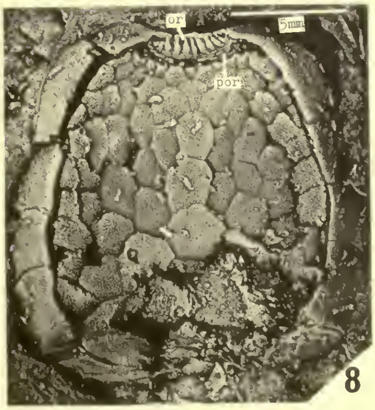

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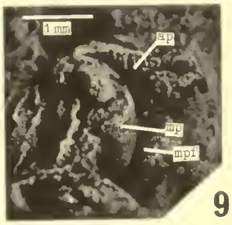
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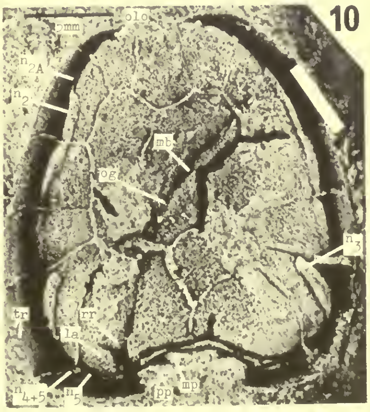
5mm
olo
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rr
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n4+5
n5
pp
mp

10

PLATE 9

Mitrocystella incipiens miloni

FIG. 1. E 28886. Natural internal mould, dorso-posterior aspect of right half. af = articular facet of M_{1RD} ; csb = carrot-shaped body (lateral-line ganglion); gpco = groove limiting posterior coelom ; mpf = medial part foramen ; n_5 = nerve n_5 of palmate complex ; pb = pyriform body ; ra = right atrium ; slp = posterior extension of soft layer into dorsal skeleton.

FIG. 2. IG 18. Same specimen as Pl. 5, figs. 1, 4. Latex cast showing oblique ridge near median branch (mb). Between the median branch and the point v, the oblique ridge was probably in contact with the anterior opening of the oesophagus.

Mitrocystella incipiens incipiens

FIG. 3. Same specimen as Pl. 7, fig. 5, but more posterior. Pyritous internal mould of posterior stem. dlc = dorsal longitudinal canal ; fdo = fragments of dorsal ossicle ventral to mc ; ic = interossicular canal ; id = infilling of ?inner interossicular depression ; lbv = lateral blood vessel ; mc = infilling of median canal (notochord).

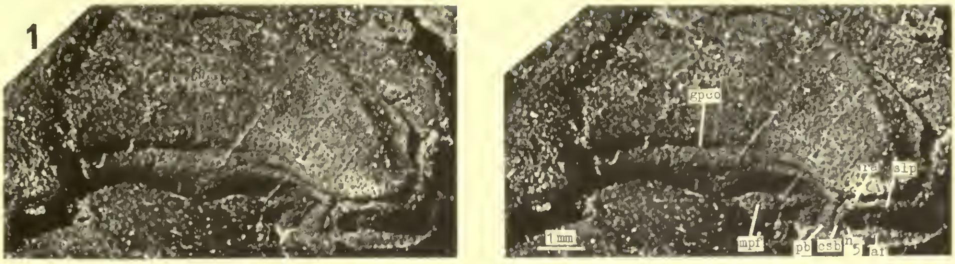
FIG. 4. IG 45d. Natural mould of external surface of M_{1RV} and M_{1RD} showing cruciform lateral line (narrow groove = ng) and part of lateral-line ganglion (carrot-shaped body = csb).

Mitrocystites mitra

FIG. 5. MCZ. 568. Šarká Beds, Osek, Czechoslovakia. Natural mould of ventral surface of dorsal ossicles of posterior stem, giving a representation of the soft parts. dnc = dorsal nerve cord; dvf = dorso-ventral facet, for reception of ventral plate ; ic = interossicular canal; lga = lateral ganglion ; not = notochord ; pig = infilling of posterior, interossicular groove.

FIG. 6. NM Akc Kat 32417/1950. Šarká Beds, Osek. Latex cast of cerebral basin, posterior aspect. lmp = part of basin carrying lower medial part of brain, i.e. inside of hypocerebral processes ; mpf = medial part foramen ; pp = part of basin carrying posterior part of brain ; ump = part of basin carrying upper medial part of brain ; w = blunt ridge on skeleton separating ump from lmp (cf. Text-fig. 27b, c, Pl. 6, fig. 62).

1


gpco
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slp
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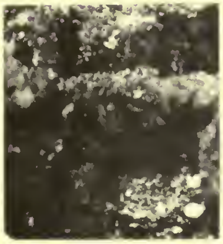
5
ar

2

1mm
mb
v

3



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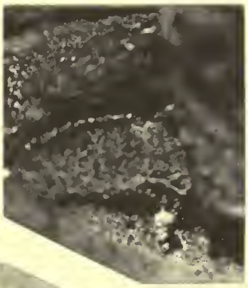

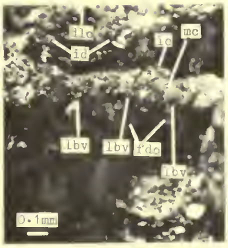
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ic
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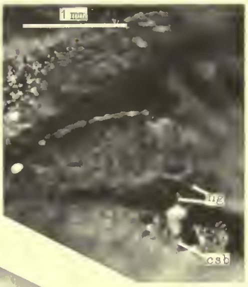
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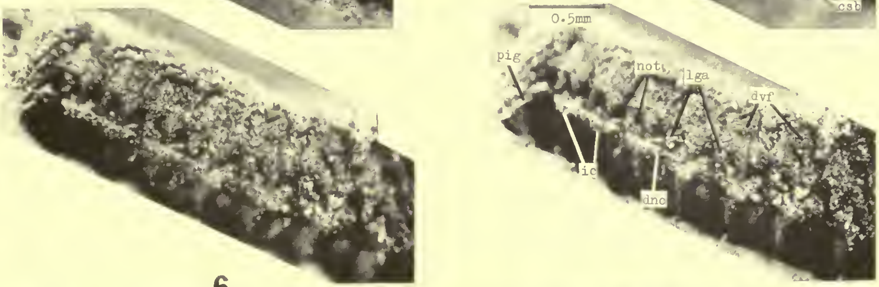
5


0.5mm
pig
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dvf
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dnc

6

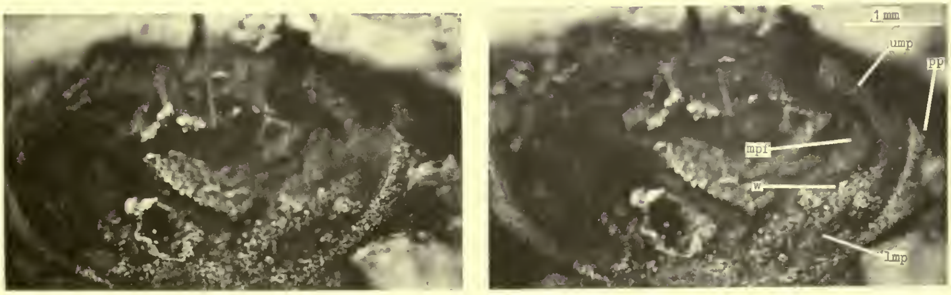
1 mm
ump
pp
mpf
w
lmp

PLATE 10

Mitrocystella incipiens miloni

FIG. 1. E 28888. Note striations (sp) on left pharyngeal chamber. grp = groove limiting right pharyngeal chamber ; n_2 = nerve n_2 ; pco = posterior coelom ; sl = soft layer of dorsal skeleton.

FIG. 2. IG 53. Natural mould. Left dorsal aspect to show typical posture with theca horizontal and posterior stem bent ventralwards. als = anterior lumen of styloid ; as = anterior stem ; ps = posterior stem.

FIG. 3. St. Andrews University, MacGregor Colln. T.3. Natural internal mould of posterior portion of theca, dorsal aspect. csb = carrot-shaped body (lateral-line ganglion); csbn = nerve to csb ; n_5,= nerve of palmate complex ; og = oblique groove ; mp = medial part of brain ; slp = posterior extension of soft layer into dorsal skeleton.

Mitrocystites mitra

FIG. 4. Same specimen as Pl. 6, fig. 8. Dorsal aspect of most of ventral and part of dorsal skeleton. il = inner layer of ventral skeleton ; ol = outer layer of ventral skeleton.

FIG. 5. MCZ 566. Šarká Beds, Osek, Czechoslovakia. Latex cast. Dorsal aspect of posterior, dorsal skeleton. Shows finer surface ornament in region of peripheral grooves (pg) than elsewhere. lp = lateral pore ; on_3 = opening of n_3 on to dorsal surface ; tr = transverse ridge.

FIG. 6. E 16058. Šarká Beds, Osek. Natural internal mould of dorsal skeleton, dorsal aspect. Note especially striations of right pharyngeal chamber (sp) and groove (grp) limiting right pharyngeal chamber on the median side. la = left atrium ; mb = median branch of oblique groove; mp = medial part of brain; n_2, n_3, n_5, n_{4+5} = nerves of palmate complex ; pco = posterior coelom ; pp = posterior part of brain ; rr = rectal ridge ; tr = transverse ridge.

FIG. 7. E 15017. Šarká Beds, Osek. Latex cast. Dorsal aspect to show stem flexed to right, probably in a fairly natural position. as = anterior stem ; lp = lateral pore ; on_3 = opening of nerve n_3 on to dorsal surface ; pg = peripheral groove ; ps = posterior stem.

FIG. 8. Same specimen as in Pl. 10, fig. 6. Internal mould of posterior part of ventral skeleton. csb = carrot-shaped body (lateralis ganglion) ; gpco = groove limiting posterior coelom ; n_3 = nerve n_3 of palmate complex in ventral skeleton ; pb = pyriform bodies (damaged in dissection) ; sl = soft layer of ventral skeleton.

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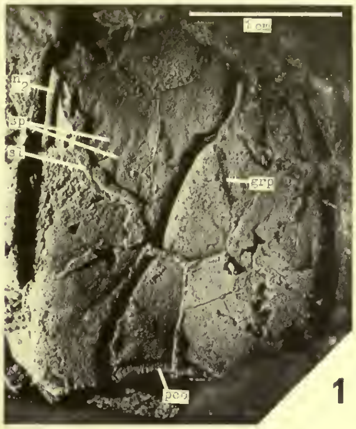
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n_2
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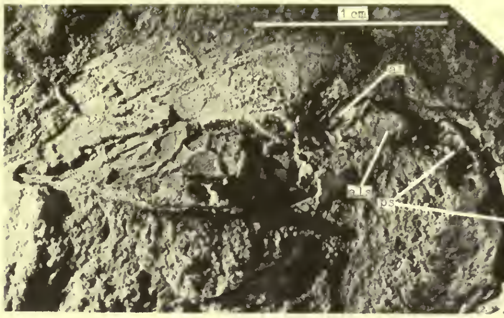
sl
grp
pco

1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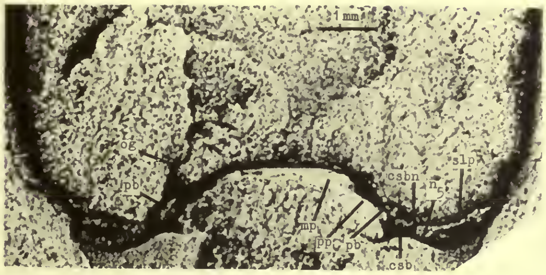
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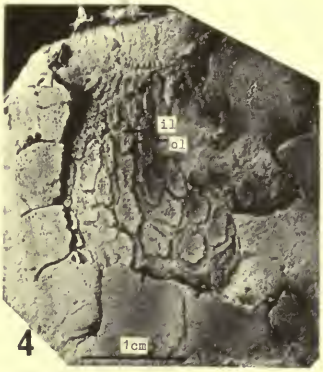
3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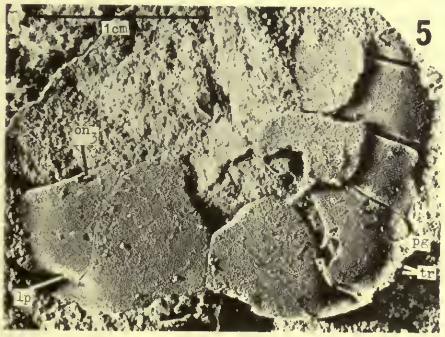
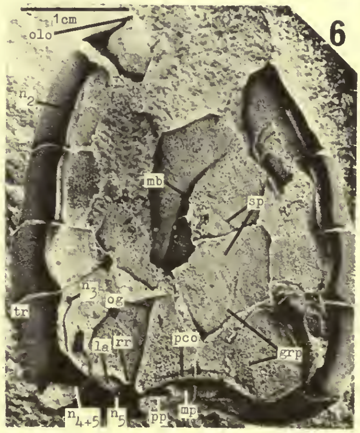

1cm
on_3
pg
tr
lp

5


1cm
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n_2
mb
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tr
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pco
grp
n_{4+5}
n_5
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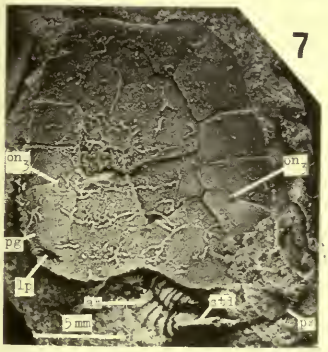
mp

6


on_3
on_3
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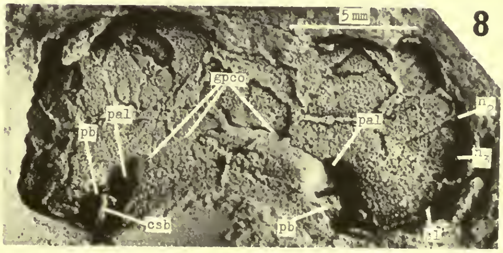
lp
s+l
5 mm
ps

7


5 mm
gpco
pal
pb
pal
n_2
n_3
csb
pb
sl

8

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PALÆONISCOIDEA-SCHUPPEN AUS DEM UNTERDEVON AUSTRALIENS UND KANADAS UND AUS DEM MITTELDEVON SPITZBERGENS

12 AUG1

HANS-PETER SCHULTZE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 7
LONDON: 1968

PALÆONISCOIDEA-SCHUPPEN AUS DEM UNTERDEVON AUSTRALIENS UND KANADAS UND AUS DEM MITTELDEVON SPITZBERGENS

BRITISH MUSEUM
12 AUG 1968
NATURAL HISTORY

BY

HANS-PETER SCHULTZE

Pp. 341–368; 4 *Plates;* 19 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 16 No. 7
LONDON: 1968

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 16, *No.* 7 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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THE BRITISH MUSEUM (NATURAL HISTORY)

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PALÆONISCOIDEA-SCHUPPEN AUS DEM UNTERDEVON AUSTRALIENS UND KANADAS UND AUS DEM MITTELDEVON SPITZBERGENS

By HANS-PETER SCHULTZE

SYNOPSIS

Zwei neue Gattungen und Arten (*Dialipina salgueiroensis* und *Ligulalepis toombsi*) der Palaeoniscoidea aus dem Unterdevon von NW-Kanada und SE-Australien sind beschrieben. Von diesen Formen sind nur Schuppen bekannt; diese Schuppen zeigen Merkmale, die von anderen Palaeoniscoidea nicht bekannt sind. Außerdem sind Schuppen von *Orvikuina* sp. aus dem Mitteldevon (Grey Hoek Schichten) von Spitzbergen beschrieben. Der unregelmäßige Verlauf der Williamson'schen Kanäle in den Schuppen von *Orvikuina* und *Dialipina* ist diskutiert. Alle Schuppen sind in Schichten marinen Ursprungs gefunden worden.

Two new palaeoniscoid genera and species–*Dialipina salgueiroensis* and *Ligulalepis toombsi*–are described from Lower Devonian rocks of Northwestern Canada and Southeastern Australia. These forms are represented only by scales which show certain characters hitherto unknown in Palaeoniscoidea. In addition scales of *Orvikuina* sp. are described from the Middle Devonian (Grey Hoek beds) of Spitsbergen. The irregular canals of Williamson in the scales of *Orvikuina* and *Dialipina* are discussed. The forms described here occur in marine rocks.

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I. EINLEITUNG

Die ältesten Palaeoniscoidea sind aus dem Mitteldevon bekannt, so ist von Interesse, aus dem Unterdevon auch Reste allein zu beschreiben. Die hier beschriebenen Palaeoniscoidea-Schuppen stammen von weit auseinanderliegenden Fundpunkten, einmal aus SE-Australien, dann aus NW-Kanada. Hinzugefügt sei eine Beschreibung von Schuppen aus dem Mitteldevon Spitzbergens, die der Gattung *Orvikuina* angehören und bisher nur aus dem baltischen Mitteldevon bekannt waren.

Die Bearbeitung des Materials erfolgte im Naturhistoriska Riksmuseet, Paleozoologiska sektionen, Stockholm. Aufbewahrt werden die Schuppen aus Australien im British Museum (Natural History), London, die Schuppen aus Kanada im National Museum of Canada, Ottawa und die Schuppen aus Spitzbergen im Naturhistoriska Riksmuseet, Paleozoologiska sektionen, Stockholm (nicht in Essigsäure aufgelöstes Gestein der gleichen Lokalität besitzen das British Museum (Natural History), London und das Paleontologiska Museum, Oslo).

Alle Schuppen wurden durch Herauslösen mit Essigsäure aus dem Gestein gewonnen. Von dem australischen Material lagen nur die isolierten Schuppen zur Bearbeitung vor (herausgelöst am British Museum (Natur. Hist.), London), dagegen von dem Material aus Kanada und Spitzbergen (Schuppen herausgelöst von Dr. T. Ørvig, Naturhist. Riksmuseet, Stockholm) auch das Gestein. In dem leicht schiefrigen Gestein aus Kanada ist eine Bearbeitung der Schuppen auch ohne Herauslösen möglich. Für die Dünnschliffe wurden die isolierten Schuppen in eine Plastikmasse eingebettet (Soredur H 75 von der Firma Svenska Oljeslageri Aktiebolaget, Göteborg). Zusätzlich wurden von dem Material aus Spitzbergen und Kanada Schliffe von Schuppen angefertigt, die noch im Gestein saßen.

Die Schuppen wurden mit einer wasserlöslichen Farbe grün gefärbt und mit Ammoniumchlorid bestäubt, bevor sie photographiert wurden. Die Aufnahmen habe ich selbst gemacht, die Abzüge davon Herr W. Wetzel, der Photograph des Geol.-Paläont. Instituts Tübingen. Die Zeichnungen wurden von Herrn C. Salgueiro, Naturhist. Riksmuseet, Stockholm angefertigt.

Für die jederzeit großzügige Unterstützung im Naturhistoriska Riksmuseet, Paleozoologiska sektionen, Stockholm möchte ich dem Direktor Herrn Professor Dr. E. Jarvik herzlich danken. Besonders stark hat Intendent Dr. T. Ørvig diese Arbeit gefördert, er hat mir das Material aus Kanada und aus Spitzbergen zur Verfügung gestellt. Viele Angaben im stratigraphischen Teil dieser Arbeit verdanke ich ihm. Das australische Material sandte Dr. C. Patterson nach Stockholm, die Erlaubnis zur Bearbeitung erteilte Dr. E. I. White, beide British Museum (Natur. Hist.), London. Mr. H. A. Toombs, British Museum (Natur. Hist.), London war so freundlich, mir ein ausführliches Verzeichnis der australischen Fundpunkte zu schicken. Professor Dr. W. Gross, Geol.-Paläont. Institut, Tübingen, war so entgegenkommend, mir Schliffe von *Orvikuina* aus Spitzbergen zur Bearbeitung zu überlassen, die er früher selbst hergestellt hatte.

Für die Anfertigung der Zeichnungen habe ich Herrn C. Salgueiro, Naturhist. Riksmuseet, Paleozool. sektionen, Stockholm sehr zu danken. Eingeführt in das oben beschriebene Photographierverfahren hat mich Dr. F. Adamczak, Geologiska institutionen der Universität Stockholm. Für die Herstellung der Abzüge danke ich Herrn W. Wetzel, Geol.-Paläont. Institut Tübingen. Dr. G. J. Nelson, American Museum, New York hat freundlicherweise die englische Zusammenfassung korrigiert.

Mein Aufenthalt in Stockholm wurde von der Deutschen Forschungsgemeinschaft finanziert.

Benutzte Abkürzungen:

BM	British Museum (Natural History), London
GrB	Schliffsammlung W. Gross aus dem Institut für Paläontologie und Museum Berlin
NMC	National Museum of Canada, Ottawa
PMO	Paleontologiska Museum, Oslo
Sto	Naturhistoriska Riksmuseet, Paleozoologiska sektionen, Stockholm
←	zeigt in den Abbildungen immer in rostraler Richtung

II. MORPHOLOGIE UND HISTOLOGIE

LIGULALEPIS nov. gen.

DEFINITION. Gattung der Palaeoniscoidea mit hohen Schuppen an den Flanken; Schuppen nahe dem Schultergürtel 3–4 mal so hoch als lang; an der vorderen oberen Ecke ein sehr markanter Fortsatz, der vom Vorderrand[1] scharfwinkelig abgesetzt ist; Ventralrand vom Vorderrand schräg nach caudal abfallend. Kräftiger Dorn und dementsprechend tiefe Grube; Kiel recht tief; zweiter " Kiel ", an dessen Hinterrand die Öffnungen der meisten Kanäle liegen.

DERIVATIO NOMINIS. ligula (lat.) = flacher Löffel (bezieht sich auf den Fortsatz an der vorderen oberen Ecke), λεπίς (griech.) = Schuppe.

Ligulalepis toombsi gen. et sp. nov.

(Abb. 1–6, Taf. I, Fig. 1–8 u. Taf. IV, Fig. 1)

DEFINITION. Als Artmerkmale seien der Gattungsdefinition vor allem die Ausbildung der Ganoinfläche hinzugefügt. Ganoinfläche stark gegliedert, zum Ventralrand hin teilweise in einzelne Rippen zerteilt, zum Vorderrand hin mit Längsleistchen verziert und in einzelne Schüppchen aufgelöst; Hinterrand pectinat; Vorderrand gerade oder schwach konkav, vordere untere Ecke abgerundet, Ventralrand gerade.

FUNDSCHICHT/-ORT. Taemas Stufe, Murrumbidgee Schichten, Unterdevon/Murrumbidgee River, New South Wales, Australien[2].

MATERIAL. 202 Schuppen und Schuppenbruchstücke, 6 Schliffe.

HOLOTYP. BM: P 48864 (Abb. 1 u. Taf. I, Fig. 4).

DERIVATIO NOMINIS. *toombsi* = zu Ehren von H. A. Toombs, der die hier beschriebenen Fossilien 1963 in New South Wales gesammelt hat.

STRATIGRAPHIE. Bei der Essigsäurepräparation der Vertebratenfossilien[3] die H. A. Toombs 1963 in der Umgebung des Murrumbidgee Rivers gesammelt hatte, kamen in den Rückständen auch kleinere Reste von Vertebraten (" Vertebraten-Mikrofossilien ") zum Vorschein, darunter auch die Schuppen von Palaeoniscoidea. Diese Palaeoniscoidea-Schuppen aus dem Unterdevon sind älter als alle bisher beschriebenen Palaeoniscoidea, Palaeoniscoidea sind erst ab dem Mitteldevon bekannt (*Orvikuina*, *Cheirolepis*). Früher wurden auch die australischen Schichten ins Mitteldevon gestellt, diese Einstufung stellte sich aber bei Überprüfung der Invertebratenfauna als unrichtig heraus (Philip, G. M. u. Pedder, A. E. M. 1964). Die Conodontenfauna der etwa gleichaltrigen Schichten im Buchan District stuft G. M. Philip 1967 ins untere Emsium ein, in derselben Arbeit stellt er die Murrumbidgee Schichten ins obere Emsium (oberstes Unterdevon). Für die Murrumbidgee Schichten gibt I. Browne 1959 folgende Einteilung:

---

[1] Begriffe benutzt wie in Schultze, H.-P. 1966, Abb. 1, S. 236.

[2] detaillierte Angaben bei den Abbildungen nach H. A. Toombs.

[3] Es handelt sich hauptsächlich um Arthrodiren; diese bearbeitet zur Zeit Dr. E. White (vergleiche dazu die Beschreibung von Arthrodiren der gleichen Fundstelle, White, E. 1952).

	Mächtigkeit in feet	Anzahl an Schuppen und –bruchstücken
Taemas Stufe:		
Feine Tuffe und Schiefer	100	—
Crinoidenkalk	500	—
Warrookalk	370	4 } ?10
Receptaculites Kalk	590	1
Bloomfieldkalk	400	6, ?1
Currajongkalk	400	?6
Spirifer yassensis Kalk . . .	400	170, ?2
Majurgong Stufe:		
Rote Schiefer, Sandsteine und Quarzite	400	—
Cavan Stufe:		
Dünnbankiger Kalk Geländestufe bildender Kalk Plattige Kalke, Schiefer und Quarzite . .	400	2
	insgesamt	202

In dieser Tabelle sind die der Arbeit zu Grunde liegenden Schuppen in ihrer stratigraphischen Verbreitung aufgeführt, für mit ? versehene Zahlen ist die stratigraphische Zuordnung fraglich. Der Hauptteil der Schuppen stammt aus dem *Spirifer yassensis* Kalk und davon die meisten (108 = 53,5 % aller Schuppen) von einem Fundpunkt nahe der Basis des *Spirifer yassensis* Kalkes. Unverhältnismäßig häufig sind unter den Schuppen die hohen Schuppen der Flanken vertreten, was wohl nur auf Auslese bei der Ablagerung beruht. Die eigentlich am Fisch zahlreicheren, mehr rhombischen Schuppen der Dorsal-, Ventral- und Caudalregion sind selten.

MORPHOLOGIE. Die hohen Schuppen zeigen zwei sehr auffällige Merkmale im Vergleich zu den Schuppen anderer Palaeoniscoidea: einen löffelförmigen Fortsatz an der vorderen oberen Ecke und einen zweiten " Kiel " auf der Innenseite. Vom geraden Vorderrand biegt an der vorderen oberen Ecke der löffelförmige Fortsatz winkelig ab (Abb. 1, 4 u. Taf. I, Fig. 4–6). Wohl ist bei rhombischen Schuppen die vordere obere Ecke oft verlängert (Taf. I, Fig. 9), bildet aber nie einen derartig breit abgerundeten Fortsatz. Dieser Fortsatz fehlt den rhombischen Schuppen vor der Caudalis (Abb. 2 u. Taf. I, Fig. 8), aber auch den besonders hohen Schuppen direkt hinter dem Schultergürtel. Diese hohen Schuppen (Abb. 3 u. Taf. I, Fig. 1, 2) besitzen auch keinen deutlich ausgebildeten Dorn. Im Gegensatz zu den Flankenschuppen, die bis 3 mal so hoch wie lang werden, erreichen diese Schuppen hinter dem Schultergürtel bis über 4fache Höhe verglichen zur rostral-caudalen Erstreckung (= Länge).

Der Dorn, recht kräftig ausgebildet, läuft von einer breiten Basis zu einer Spitze aus (Taf. I, Fig. 5, 6). Er greift in eine tiefe Grube (Abb. 1b u. Taf. I, Fig. 4b), die zwischen Kiel und zweitem " Kiel " liegt. Von der Grube zur Mitte des Dornes

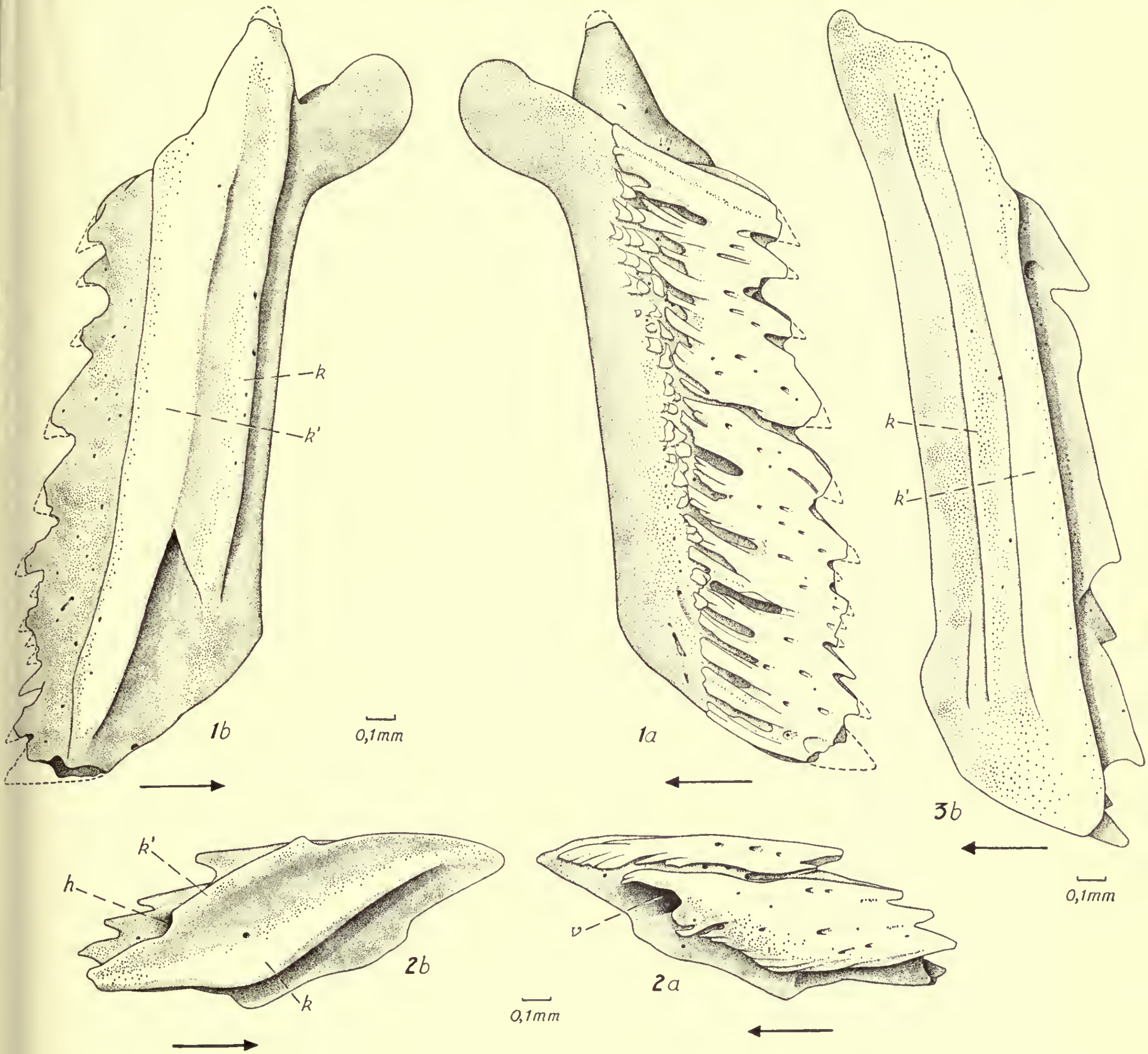

ABB. 1, 2, 3b. *Ligulalepis toombsi* n.g. n. sp., Unterdevon, New South Wales, Australien. 1. BM: P 48864. Holotyp. *Spirifer yassensis* Kalk (unterer Teil), " right bank of Murrumbidgee, boulders probably nearly *in situ*, on shore and up hillside, 2500 yds. due E. of Majurgong T.S. " Hohe Schuppe aus der vorderen Körperhälfte der linken Körperseite. a, Außenseite. b, Innenseite. ×40. 2. BM: P 48849. Bloomfield Kalk, " not *in situ*, on hillside south of inlet, 2750 yds at 4° magnetic from Majurgong T.S. " Seitenlinienschuppe aus der hinteren Körperhälfte der linken Körperseite. a, Außenseite. b, Innenseite. ×40. 3b, BM: P 48853. *Spirifer yassensis* Kalk (unterer Teil), Lokalität wie P 48864 (= Abb. 1). Hohe Schuppe aus der Region dicht hinter dem Schultergürtel, rechte Körperseite. Innenseite. ×40.

k = Kiel, k′ = zweiter " Kiel ", v = vordere und h = hintere Öffnung des Seitenlinienkanals.

verläuft eine Rinne, die Kiel und zweiten " Kiel " trennt. Nur der erste Kiel wird von Sharpey'schen Fasern durchzogen (Abb. 6), wie es dem echten Kiel rhombischer Schuppen entspricht. Der zweite " Kiel " ist frei von Sharpey'schen Fasern, an seiner Hinterkante münden Kanäle des Kanalsystems aus (Taf. I, Fig. 7). Das Größenverhältnis zwischen Kiel und zweitem " Kiel " verschiebt sich von den Schuppen nahe des Schultergürtels zu denen nahe der Caudalis. Während der Kiel der Schuppen nahe des Schultergürtels schmal und flach ist, nimmt er zu den rhombischen Schuppen vor der Caudalis hin an Breite zu und übertrifft den zweiten " Kiel " (Abb. 2b u. Taf. I, Fig. 8b). Der Kiel erreicht die Tiefe des zweiten " Kieles " oder die Schuppe ist an dieser Stelle sogar dicker.

Der Vorderrand verläuft meist auffallend gerade, Dorsal- und Ventralrand fallen schräg nach caudal ab. Der Hinterrand ist pectinat gezackt.

Das freie Feld (= nicht von benachbarten Schuppen überdeckter Teil) der Schuppen ist reich gegliedert. Bei den hohen Schuppen ist die Ganoindecke nur nahe dem Hinterrand geschlossen, besonders zum Ventralrand hin ist sie in einzelne Rippen aufgeteilt. Die Furchen zwischen diesen Rippen können bis auf die Knochenbasis hinabreichen. Zum Vorderrand hin ist die Ganoindecke in einzelne Schüppchen aufgelöst, die über die Schuppenoberseite aufragen, das dahinter liegende Ganoin überragen und überdecken (Abb. 1a u. Taf. I., Fig. 4a, 5). Die Schüppchen sind also jünger als das dahinter liegende Ganoin. Vor allem nahe dem Vorderrand ist das Ganoin, ganz gleich ob es sich um eine geschlossene Ganoindecke (Abb. 2a u. Taf. I, Fig. 8a), Rippen (Abb. 3a u. Taf. I, Fig. 1a) oder Schüppchen (Taf. I, Fig. 2a, 3, 5, 6a) handelt, mit kräftigen Längsleistchen verziert.

Besonders auf der geschlossenen Ganoindecke fallen zahlreiche Poren auf, die in Reihen parallel zum Ventral- bzw. Dorsalrand angeordnet sind (Abb. 1a, 2a). Sie liegen im ventralen Abschnitt der hohen Schuppen in den Furchen zwischen den Rippen; gelegentlich sind sie außerdem parallel zum Hinterrand aufgereiht (Abb. 3a u. Taf. I, Fig. 1a, 3). Die Poren sind die Öffnungen der Kanäle, die von den Querkanälen zwischen den großen Kanalräumen aufsteigen (Abb. 4 u. Taf. IV, Fig. 1). Die großen Kanalräume sind parallel zu Ventral- bzw. Dorsalrand angeordnet, entsprechen dem Verlauf der mit Ganoin bedeckten Rippen, unter denen die Kanalräume liegen. In der gleichen Weise, wie die Kanalräume den Rippen folgen, ziehen sie auch in die größeren Schüppchen hinein, so daß unter dem vorderen dorsalen Abschnitt des freien Feldes ein mehrschichtiges Kanalsystem entsteht. Das Kanalsystem ist auf den mittleren Bereich der Schuppe beschränkt. Rostralwärts endet es vor dem mit Ganoin bedeckten freien Feld, wo zahlreiche Poren ausmünden. Caudalwärts münden die meisten Kanäle am Hinterrand des zweiten " Kieles " aus (Taf. I, Fig. 7), nur wenige reichen in die Zacken des Hinterrandes hinein.

Abb. 2 (= Taf. I, Fig. 8) zeigt eine Seitenlinienschuppe aus der hinteren Körperhälfte mit deutlich sichtbarer vorderer Öffnung des Seitenlinienkanals, während die hintere Öffnung vom Hinterrand des zweiten " Kieles " verdeckt wird. Außer dieser rhombischen Seitenlinienschuppe enthielt das Material zwei schlecht erhaltene Seitenlinienschuppen, die höher als lang sind. Die hohen Schuppen selbst werden **nicht** vom Seitenlinienkanal durchzogen. Der schräge Schlitz im oberen Abschnitt der hohen Schuppe BM: P 48851 (= Taf. I, Fig. 2) markiert die Öffnung des Grübchenorgans (danach ist es wahrscheinlich, daß diese Schuppe im vorderen dorsalen Körperabschnitt lag), sie enthält aber keinen Seitenlinienkanal.—Die Seitenlinie verläuft entweder ventral oder dorsal der hohen Schuppen an der Flankenmitte.

Histologie. Für histologische Untersuchungen ist das Schuppenmaterial sehr ungünstig erhalten, aber nach einigen Schliffen läßt sich die Innenstruktur abklären (Abb. 5, 6). Die Schuppen zeigen den typischen Aufbau einer palaeoniscoiden Ganoidschuppe mit Knochen-, Dentin- und Ganoinschicht. Die Knochenschicht ist durch Kiel und zweiten " Kiel " verhältnismäßig dick. Eine Schichtung der Knochenschicht ist zu beobachten, Knochenzellen sind ausgebildet, Williamson'sche Kanäle konnten nicht festgestellt werden. Die Sharpey'schen Fasern sind auf den

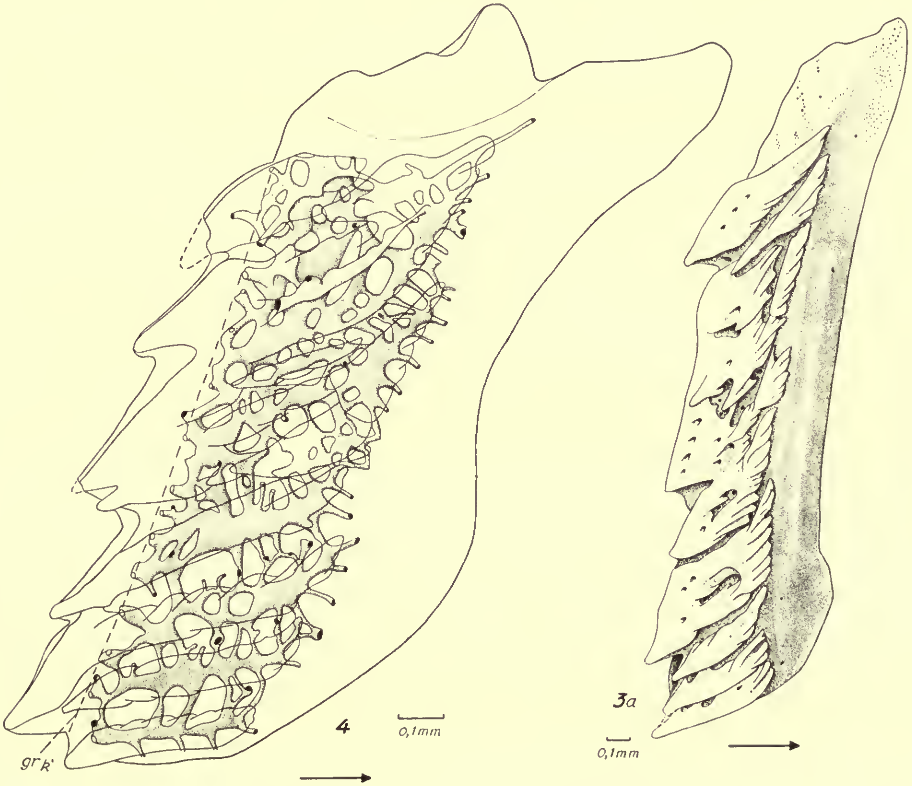

Abb. 3a, 4. *Ligulalepis toombsi* n.g. n. sp., *Spirifer yassensis* Kalk, Unterdevon, New South Wales, Australien. 3a, BM: P 48853. " Right bank of Murrumbidgee, boulders probably nearly *in situ*, on shore and up hillside, 2500 yds. due E. of Majurgong T.S. " Hohe Schuppe aus der Region dicht hinter dem Schultergürtel, rechte Körperseite. Außenseite. ×32. 4, BM: P 48855. " Top of spur falling west to left bank of Murrumbidgee, 1800 yds. at 347° magnetic from Majurgong T.S. " Hohe Schuppe der rechten Körperseite etwa aus der Körpermitte, dargestellt das Kanalsystem, die höher liegenden Kanäle heller. ×60. $gr_{k'}$ = Hinterrand des zweiten " Kieles ".

● = Öffnungen der Kanäle auf der Schuppenoberseite, ○ = Öffnungen der Kanäle auf der Schuppeninnenseite.

(ersten) Kiel beschränkt natürlich abgesehen davon, daß sie am Dorsal- und Ventralrand der Schuppen wie in allen rhombischen Schuppen zu finden sind. Über der Knochenschicht liegt das stark ausgebildete Kanalsystem. Die Dentinröhrchen steigen nicht direkt von den Kanälen als Ausläufer je eines Odontoblasten nach oben auf. Vielmehr gehen von den großen Kanälen relativ dünne Röhrchen (aber dicker als die am Ende verästelten Dentinröhrchen) aus, die sich verzweigen und dann parallel zu den Wachstumszonen des Dentins verlaufen. Von diesen parallel den Wachstumszonen verlaufenden Röhrchen zweigen erst die Dentinröhrchen nach oben ab, die sich an den Enden verästeln. Aber auch die parallel den Wachstumszonen verlaufenden Röhrchen verästeln sich an den Enden. Die einzelnen Dentinbereiche sind gegeneinander durch Resorptionslinien abgegrenzt. Etwas überraschend ist, daß eine Skulpturrippe nicht einem Dentinbereich entspricht, sondern daß das Dentin der ventral nächsten Rippe auf die dorsal gelegene übergreift. Die Resorptionslinie verläuft senkrecht durch eine Skulpturrippe (Abb. 5). Das Ganoin ist dünn und wahrscheinlich einschichtig, da keine Schichtung beobachtet werden konnte.

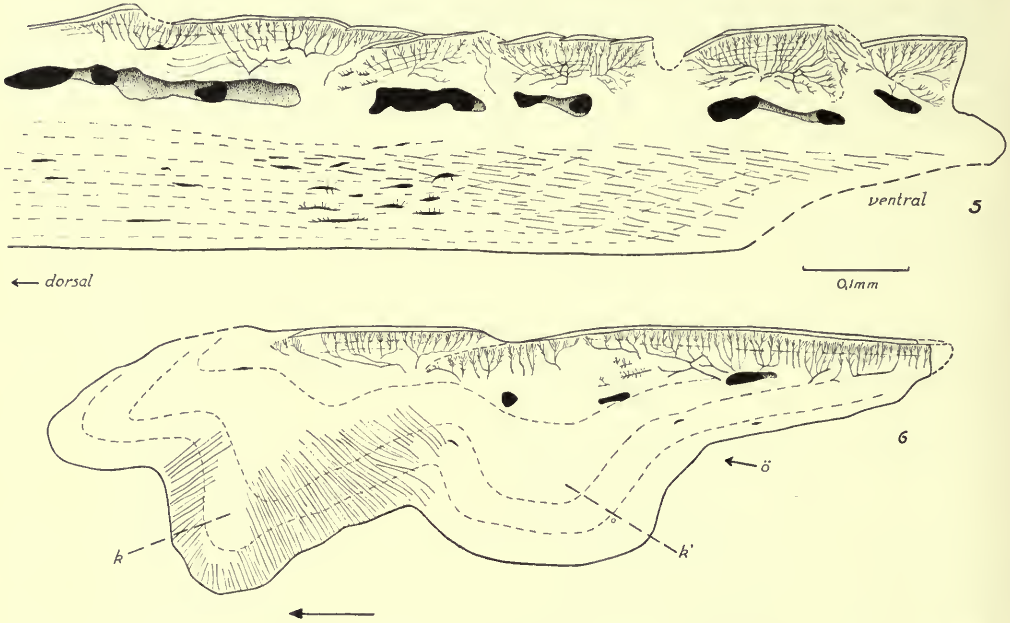

Abb. 5, 6. *Ligulalepis toombsi* n.g. n. sp., *Spirifer yassensis* Kalk, Unterdevon, " left bank of Murrumbidgee, rock face in gully 1200 yds. at 39° magnetic from Majurgong T.S. " New South Wales, Australien. 5, BM: P 48842. Ventraler Abschnitt eines dorsal-ventralen Vertikalschliffes, × 140. 6, BM: P 48841. Rostral-caudaler Vertikalschliff, × 140.

k = Kiel, k′ = zweiter " Kiel ", ö = Gebiet, wo die Kanäle nach caudal aus der Schuppe ausmünden.

Vergleiche. Innerhalb der Palaeoniscoidea gibt es keinen Fisch mit hohen Schuppen der Gestalt wie *Ligulalepis*. Nur im rostral-caudalen Vertikalschliff erhält man eine Vergleichsmöglichkeit und zwar überraschenderweise mit den geometrisch rhombischen Schuppen von *Cheirolepis*. Schneidet man eine *Cheirolepis*-Schuppe in der Richtung der Körperlängsachse (= Diagonale der Schuppe), so erhält man ebenfalls einen Kiel mit Sharpey'schen Fasern und einen zweiten " Kiel ", an dessen Hinterrand wie bei *Ligulalepis* das Kanalsystem ausmündet (Taf. I, Fig. 10 u. Aldinger, H. 1937, Abb. 50B, S. 197). Hier wird der zweite " Kiel " allerdings im Gegensatz zu *Ligulalepis* in seinem vorderen Abschnitt von Sharpey' schen Fasern durchsetzt, ist aber am Hinterrand völlig frei von Sharpey'schen Fasern. Auch hier verliert die Schuppe hinter dem zweiten " Kiel " stark an Dicke, der rostrale Abschnitt ist aber anders als bei *Ligulalepis* geformt. Das Kanalsystem liegt im dorsalen Abschnitt der hohen Schuppen von *Ligulalepis* wie bei *Cheirolepis* in verschiedenen Ebenen. Knochenzellen sind in der Knochenschicht beider Gattungen ausgebildet, das Fehlen Williamson'scher Kanäle ist beiden Gattungen ebenfalls gemeinsam.

Diesen Ähnlichkeiten der Schuppen von *Ligulalepis* und *Cheirolepis* im rostral-caudalen Schnittbild stehen aber große Unterschiede im Hartgewebe und der Schuppenform gegenüber. So ist bei *Cheirolepis* das Ganoin mehrschichtig, bei *Ligulalepis* nur einschichtig. In den Schuppen von *Cheirolepis* reichen die Dentinröhrchen zwischen die Ganoinlamellen, sie zweigen direkt von den Kanälen ab und nicht erst von dünnen Röhrchen wie bei *Ligulalepis*. Nicht zu übersehen ist der Unterschied in der Form der Schuppen beider Palaeoniscoidea-Gattungen. So mag das gleiche Schnittbild nur eine Zufälligkeit sein und nicht auf verwandtschaftliche Beziehungen hinweisen.

Das Kanalsystem von *Ligulalepis* zeigt im ventralen Abschnitt der hohen Schuppen eine Anordnung wie das Kanalsystem in *Aetheretmon valentiacum* White (Aldinger, H. 1937, Abb. 91, S. 305). Hier folgen weite Kanäle den Skulpturrippen, von denen kurze und viel schmälere Querkanäle abzweigen. T. Cavender 1963 bezeichnet diese Kanalanordnung als *Aetheretmon*-Typ (Cavender, T. 1963, Taf. V, Fig. F) und sieht sie vertreten bei *Aeth. valentiacum* White, *Haplolepis tuberculata* (Newberry) und einigen *Rhadinichthys*-Arten. Im dorsalen Abschnitt der Schuppen von *Ligulalepis* findet man diese Regelmäßigkeit in der Kanalanordnung nicht.

DIALIPINA nov. gen.

Definition. Gattung der Palaeoniscoidea mit annähernd gleich hohen wie langen Schuppen an den Flanken. Ganoin nur auf den isolierten Rippen ausgebildet; caudalwärts enden die Rippen in Spitzen, und zwischen diesen legt sich die neue Ganoingeneration in alternierend sitzenden Flecken an. Kräftiger Dorn, aber flache Grube auf der Innenseite; Kiel nur schwach ausgebildet und vor der Verbindungslinie Grube-Dorn liegend. Außer Schuppen ein Knochenstück bekannt, dessen Oberfläche nur mit Ganoinflecken verziert ist. Unregelmäßiger Verlauf der Williamson'schen Kanäle.

DERIVATIO NOMINIS. *διαλει′πειν* (griech.) = dazwischenstehen (bezieht sich auf die alternierende Stellung der Ganoinflecken nahe dem Hinterrand).

Dialipina salgueiroensis gen. et sp. nov.

(Abb. 7-11, Taf. I, Fig 9 u. Taf. II)

DEFINITION. Die mit Ganoin bedeckten Rippen laufen im vorderen Teil des freien Feldes etwa parallel dem Vorderrand, biegen dann nach caudal ab, um dann dem Ventralrand zu folgen. Verzierung der Ganoinrippen im vorderen, dem Vorderrand parallel verlaufenden Abschnitt mit feinen Längsleistchen, diese auch auf den Ganoinflecken des Knochenstückes; der Hinterrand der Ganoinflecken nahe dem Vorderrand des Knochenstückes fein gezackt. Hinterrand der Schuppen unregelmäßig serrat.

FUNDSCHICHT/-ORT. ?Delorme Formation, Unterdevon/Anderson River, Nordwestkanada.

MATERIAL. 205 Schuppen und Schuppenbruchstücke (22 isoliert, die übrigen auf dem Gestein), 1 Knochenbruchstück, 12 Schliffe.

HOLOTYP. NMC 11608 (Abb. 7 u. Taf. II, Fig. 2).

DERIVATIO NOMINIS. *salgueiroensis* = zu Ehren von C. Salgueiro, dem Zeichner aller Abbildungen dieser Arbeit.

STRATIGRAPHIE. Das von Dr. A. C. Lenz, Standard Oil, California gesammelte Material wurde von Dr. D. Baird, Princeton, USA an Dr. T. Ørvig, Stockholm zur Bestimmung geschickt. 1962 hat ein Student (N.-A. Mörner) das Material im Rahmen einer Examensarbeit durchgesehen, veröffentlicht wurde aber bisher nur ein gut erhaltener Dipnoer-Unterkiefer (Jarvik, E. 1967). Als Unterlage zur genauen Bestimmung des Alters der devonischen Schichten am Anderson River existiert keine Untersuchung der Invertebratenfauna, zitiert seien daher die Angaben des National Museum of Canada:

" *Outcrop locality* AR.25.58. of Mr. Ben Moore's Anderson River traverse (made in the Summer of 1958 by boat).

Location—Latitude 68° 11′ North 125° 49′ West—on Anderson River just upstream from Junction with Ross River.

The strata as described by Mr. Moore are as follows, measured from the base of the outcrop *upwards stratigraphically*:

50 feet Black, calcareous shales and shaly limestone, slabby to flaggy rarely massive with abundant fish remains and possible small brachiopods with bands of limestone, microcrystalline, blocky, medium grey coloured also containing fish remains.

20 feet Limestone cryptocrystalline, medium dark grey coloured.

50 feet Dolomite breccia and limestone.

This outcrop is separated by a covered interval from apparently underlying strata (thickness not stated) which contains fossils identified by Dr. D. J. McLaren as ?*Halysites* sp. and *Catenipora* sp. (Locality AR.11.58) and *Favosites* sp., *Halysites* sp. with *Lambeioceras lambi* (Locality AR.1.58). The fish remains of AR.25.58 were considered to be " possibly Lower Devonian " by Dr. McLaren. The outcrop is apparently overlain after a covered interval (thickness not stated), by strata which include the brachiopod *Schuchertella nevadensis* identified by Dr. D. J. McLaren (Locality AR.56.58).

The shales and limestones of AR.25.58 have been tentatively correlated with the Delorme Formation[1]. The overlying breccia is possibly correlative with the Bear Rock Formation[2]. "

N.-A. Mörner 1962 kam bei der Durchsicht des gesamten Fossilmaterials (Acanthodii, Cladoselachiidae, Palaeoniscoidea, Porolepiformes, Dipnoi, Conchostraca, Ostracoda, Brachiopoda, Conodonta und Charophyta) zu der Auffassung, daß das Vorkommen in das oberste Unterdevon oder unterste Mitteldevon einzustufen sei (S. 13). Die Invertebraten sind zu schlecht erhalten, um sie zu einer Altersbestimmung heranziehen zu können. Die Pflanzen (Charophyta, von B. Lundblad, Palaeobotaniska sektionen, Naturhistoriska Riksmuseet, Stockholm bestimmt als " *Trochiliscus* sp. " und " *Sycidium* sp. ") lassen eine genaue Einstufung auch nicht zu, ähnliche Funde aus Kanada sind der Onondaga Formation, oberstes Unterdevon, zugeordnet worden (Peck, R. E. 1953, S. 212).

Es stehen sich also zwei Ansichten über das Alter der Schichten gegenüber (oberstes oder unterstes Unterdevon).

MORPHOLOGIE. Das besonders Auffällige der Schuppen von *Dialipina* ist der alternierende Zuwachs der mit Ganoin bedeckten Flecken am Hinterrand der Schuppe. Im vorderen Teil des freien Feldes laufen die Ganoinrippen etwa parallel zum Vorderrand, biegen dann nach caudal um und setzen dann etwa parallel zum Ventralrand fort. Diese Rippen werden caudalwärts nicht mehr verlängert, sondern Dentin + Ganoin werden in Flecken zwischen ihnen angelegt. Auch die weiter folgenden Flecken werden alternierend zu den vorher angelegten angeordnet. Man kann einzelne Zuwachszonen der Flecken verfolgen, die der Abfolge der Rippen nahe dem Ventralrand entsprechen (2, 3, 4 in Abb. 7c). Der Zuwachs der Flecken verlagert sich zum oberen hinteren Schuppenabschnitt. In den symmetrischen Schuppen erfolgt dagegen der Zuwachs immer symmetrisch zur Längsachse der Schuppe.

Feine Längsleistchen, die etwa parallel zum Ventralrand verlaufen, verzieren die Rippen besonders im vorderen zum Vorderrand parallel verlaufenden Abschnitt. Die Rippen steigen im vorderen, zum Vorderrand parallel verlaufenden Abschnitt langsam nach caudal an, um dann steil abzufallen. Diese Steilkante zieht hinter dem Umbiegen der Rippen in caudale Richtung auf die Mitte der Rippen und auf die Spitze am Ende zu. Manchmal zeigen auch die Flecken eine derartige Kante in der Mitte.

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[1] oberstes Silur bis unterstes Unterdevon.

[2] Mitteldevon.

Die Schuppen an den Körperflanken sind etwa gleich hoch wie lang (Abb. 7, Taf. I, Fig. 9 u. Taf. II, Fig. 2), werden langgestreckter zur Ventralregion und zur Caudalis hin (Taf. II, Fig. 3). Der Vorderrand ist gerade und schräg nach caudal geneigt. Die vordere obere Ecke ist lang ausgezogen, ohne vom Dorsal- oder Vorderrand winkelig abgesetzt zu sein. Die vordere untere Ecke ist abgerundet, der gerade Vorderrand geht allmählich in den nach ventral ausschwingenden Ventralrand über. Der Hinterrand ist unregelmäßig serrat gezackt. Ein kräftiger Dorn sitzt dem Dorsalrand auf, er verliert von seiner Basis bis zur Spitze nur wenig von seiner Breite und endet breit abgerundet. Dem kräftigen Dorn entspricht auf der Innenseite eine ebenso breite, aber relativ flache Grube. Die gesamte Schuppe ist überhaupt im Verhältnis zu ihrer Größe recht dünn. Der Kiel tritt nur schwach hervor, er verläuft vor der Verbindungslinie Grube-Dorn.

Relativ häufig sind in dem Material symmetrisch oder nahezu symmetrisch gebaute Schuppen (20 = 10% aller Schuppen). Bei den symmetrischen Schuppen (11) handelt es sich um die Schuppen der dorsalen und der ventralen Mittellinie, die etwas asymmetrischen Schuppen (9) liegen vor den Ansatzstellen der Flossen und vor der Analöffnung (Taf. II, Fig. 1).

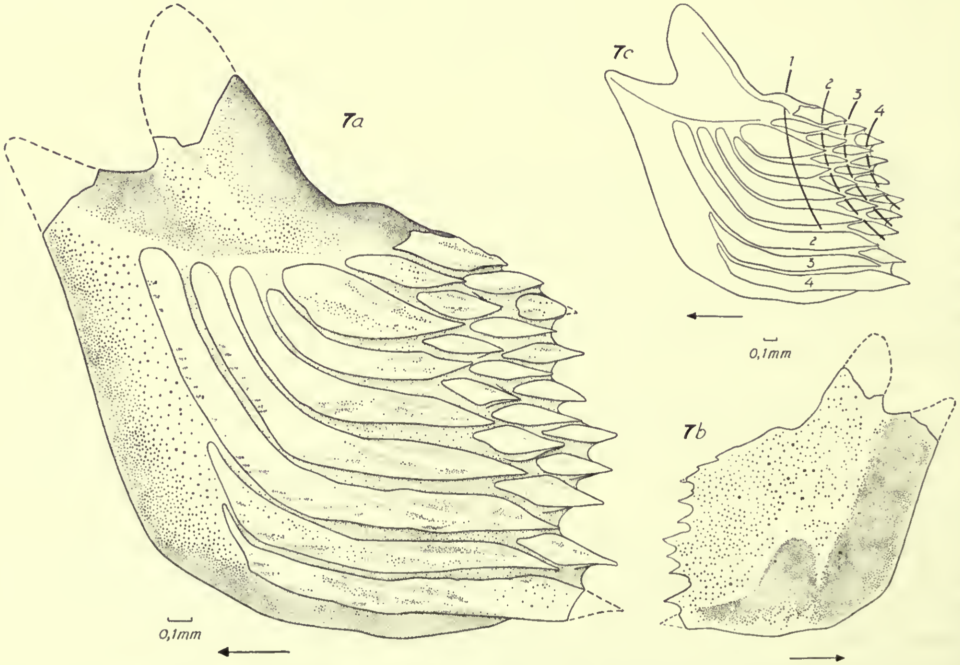


Abb. 7. *Dialipina salgueiroensis* n.g. n. sp., NMC 11608, Holotyp, Unterdevon, ?Delorme Formation, Anderson River, gerade stromaufwärts des Zusammenflusses mit dem Ross River (68° 11′ Nord/125° 49′ West), Nordwestkanada. Schuppe aus der vorderen Körperhälfte der linken Körperseite. a, Außenseite, ×32. b, Innenseite, ×16. c, Schema der Wachstumsabfolge, 1–4 = Zuwachszonen am Hinterrand, ×16.

Fig. 4 (Taf. II) zeigt ein Knochenstück, das nur eine natürliche Begrenzung besitzt—die schwach S-förmig gebogene Vorderkante. Alle übrigen Begrenzungen sind Bruchkanten. Die Orientierung erfolgte auf Grund der Längserstreckung der größeren Flecken (im hinteren Teil), die auch reich mit feinen Längsleistchen verziert sind. Die Flecken sind nur im hinteren Teil größer und flacher, im vorderen sind sie auf die ganze Erstreckung parallel zum Vorderrand klein und nach caudal steil aufgerichtet. Der Hinterrand dieser vorderen Schüppchen ist fein gezackt. Auf der Innenseite des Knochenstückes verläuft ein Wulst von der Mitte des dorsalen Teiles nach ventral an den Vorderrand. Wahrscheinlich ist dies Knochenstück ein Teil des Schultergürtels (?Cleithrum). Es zeigt, daß die Kopfknochen von *Dialipina* mit einzelnen Ganoinflecken verziert sind.

Das Kanalsystem (Abb. 11) folgt der mit Ganoin bedeckten Skulptur. Weite Kanäle folgen den Rippen vom Anfang bis nahe an die Spitze am Ende, kurz vor der Spitze verdickt sich der Kanal. Von diesen Hauptkanälen zweigen etwa rechtwinklig schmälere Querkanäle ab, die zum Teil nur über den Rand der Rippe hinausragen und dort ausmünden. Einige der Querkanäle stellen die Verbindung zum Hauptkanal der benachbarten Rippe her. Etwas unregelmäßiger scheint das

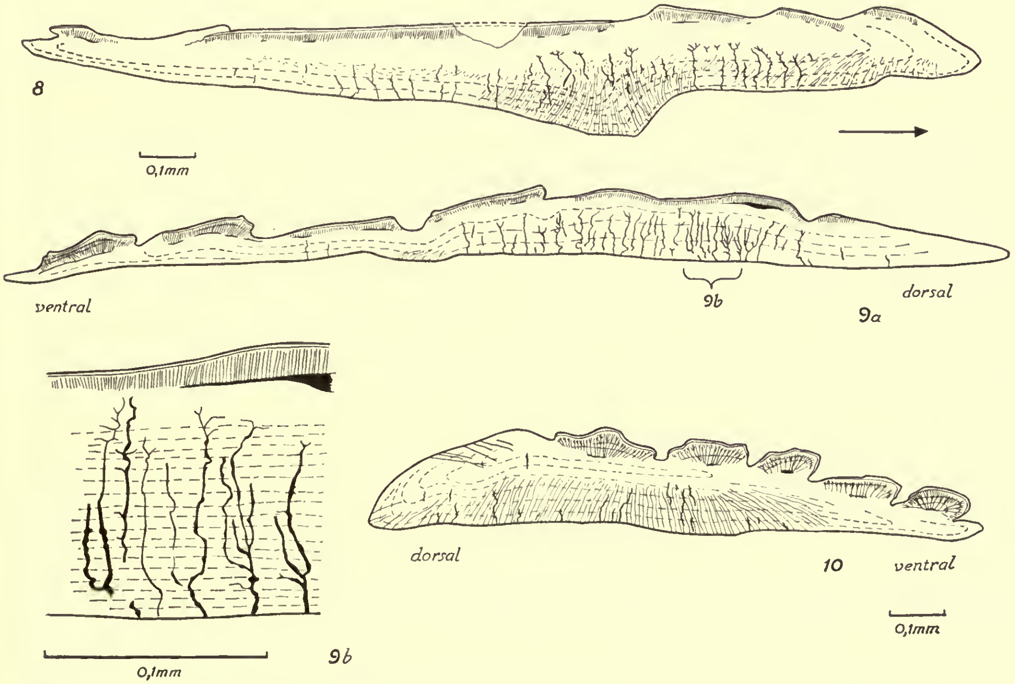


ABB. 8–10. *Dialipina salgueiroensis* n.g. n. sp., Unterdevon, ?Delorme Formation, Anderson River, gerade stromaufwärts des Zusammenflusses mit dem Ross River (68° 11′ Nord/125° 49′ West), Nordwestkanada. 8, NMC 11607. Rostral-caudaler Vertikalschliff, ×75. 9a, NMC 11606. Dorsal-ventraler Vertikalschliff, ×75. 9b, Ausschnitt aus Abb. 9a, um die Williamson'schen Kanäle zu zeigen, ×300. A. 10, NMC 11605. Dorsal-ventraler Vertikalschliff durch den Kiel. ×75.

Kanalsystem in der Nähe der Flecken zu sein. In den Flecken selbst sieht man den Hauptkanal sich verdicken wie in den Spitzen der Rippen.

Histologie. Die Schuppen bestehen zum größten Teil aus der Knochenschicht. Ganoin- und Dentinschicht sind im Verhältnis dazu recht dünn. Der dünne Ganoinbelag zeigt keine Schichtung, oft erkennt man die Ganoinschicht erst in polarisiertem Licht (Taf. IV, Fig. 6, 7). Die Dentinröhrchen sind regelmäßig unter der gesamten Ganoinschicht ausgebildet, sie gehen von den Kanälen bzw. dem Niveau des Kanalsystems aus (deutlicher Farbunterschied gegenüber der Knochenbasis). Unter dem Kanalsystem wurden keine Dentinröhrchen beobachtet. Die Kanäle sind in den meisten Schuppen recht flach, was zumindest zum Teil auf Einwirkung bei der Fossilisation (Setzung des schiefrigen Gesteins) zurückzuführen ist. Nur gelegentlich findet man Schuppen im Gestein, die höhere Kanäle zeigen (Taf. IV, Fig. 7). Die Knochenbasis ist geschichtet, es fehlen Knochenzellen, dafür sind Williamson'sche Kanäle sehr zahlreich (Abb. 8, 9). Die Williamson'schen Kanäle haben einen unregelmäßigen Verlauf, sie wechseln in ihrem Verlauf sehr in ihrer Dicke, verzweigen sich und senden gelegentlich kurze Fortsätze ab, zahlreicher gegen das Ende zu (Abb. 9b). Sie stehen nicht in Verbindung mit dem Kanalsystem oder den Dentinröhrchen. Einen gestreckteren Verlauf zeigen die Williamson'schen Kanäle, die von oben (außen) in die Knochenbasis einstrahlen und sich nur am Ende verzweigen (Abb. 10). Ihr Verlauf entspricht dem der Williamson'schen Kanäle in allen rhombischen Ganoidschuppen.

Vergleiche. Einzelne Skulpturrippen, die wie bei *Dialipina* isoliert auf der Knochenbasis sitzen, zeigen die Schuppen von *Aetheretmon whitei* Moy-Thomas (Moy-Thomas, J. A. 1938, Abb. 6, S. 315) und teilweise *Orvikuina* (Abb. 13a). Beiden Formen fehlt aber die alternierende Anlage der Flecken nahe dem Hinterrand, der Hinterrand der Schuppen von *Aeth. whitei* ist gerade. Eine auffällige Übereinstimmung im Verlauf der Skulpturrippen im vorderen Teil des freien Feldes zeigt *Strepheoschema fouldenensis* White (White, E. 1927, Abb. 45, S. 283)—so auch viele *Rhadinichthys*-Arten—die feinen Längsleistchen sind ebenfalls vorhanden. Aber auch hier ist keine Andeutung einer alternierenden Anlage von Flecken am Hinterrand zu finden, vielmehr wird im Gegenteil der hintere Teil des freien Feldes von einer geschlossenen Ganoinfläche bedeckt.

Der histologische Bau der Schuppen von *Dialipina* zeigt in der auffälligsten Struktur, den unregelmäßigen Williamson'schen Kanälen, Ähnlichkeit mit *Orvikuina vardiaensis* Gross (Gross, W. 1953, Abb. 9, 12, 13), auch fehlen bei beiden Formen die Knochenzellen. Der Aufbau des Kanalsystems aus Längskanälen, von denen Querkanäle abzweigen, ist bei beiden Formen der gleiche. Man kann das Kanalsystem von *Dialipina* ebenfalls dem *Aetheretmon*-Typ (siehe S. 351) zuordnen, nur ist der Unterschied im Lumen zwischen Längs- und Querkanälen nicht so groß wie bei *Aetheretmon*. *Orvikuina* und *Dialipina* unterscheiden sich in der Ausbildung des Dentins, vor allem treten bei *Dialipina* unter dem Kanalsystem keine Dentinröhrchen auf, in der Anlage der Skulpturrippen und in der Schuppenform. Mit dem Überlagern der Skulpturrippen ist bei *Orvikuina* ebenfalls ein mehrschichtiges Kanalsystem verbunden, beides fehlt den Schuppen von *Dialipina*. Daß *Orvikuina* vor allem langgestreckte Schuppen gegenüber den mehr quadratischen von *Dialipina* besitzt, mag kein schwerwiegender Unterschied sein, aber das Fehlen einer Dorn-Grube-Gelenkung bei *Orvikuina* steht doch in starkem Gegensatz zu der Ausbildung eines kräftigen Dornes bei *Dialipina*. Trotzdem scheint *Orvikuina* auf Grund des histologischen Baues die Gattung innerhalb der Palaeoniscoidea zu sein, die *Dialipina* am nächsten steht.

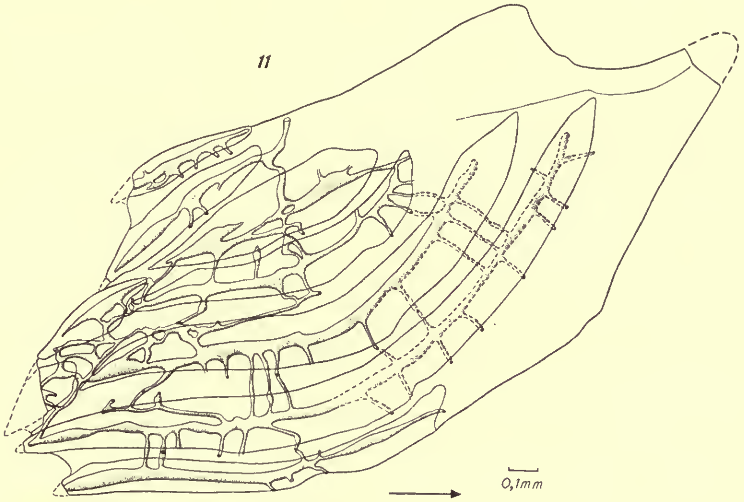


Abb. 11. *Dialipina salgueiroensis* n.g. n. sp., NMC 11611, Unterdevon, ?Delorme Formation, Anderson River, gerade stromaufwärts des Zusammenflusses mit dem Ross River (68° 11′ Nord/125° 49′ West), Nordwestkanada. Schuppe der rechten Körperseite, vermutlich aus der Körpermitte (= Taf. II, Fig. 3), dargestellt das Kanalsystem. ×40.

● = Öffnungen der Kanäle auf der Schuppenoberseite, ○ = Öffnungen der Kanäle auf der Schuppeninnenseite.

Orvikuina sp.

(Abb. 12-19, Taf. III u. Taf. IV, Fig. 4)

Fundschicht/-ort. Grey Hoek Schichten, unteres Mitteldevon/Westteil der Nordseite von V-Vaerdalen, Wood Bay, Spitzbergen.

Material. 573 Schuppen und Schuppenbruchstücke, 13 Bruchstücke von Deckknochen des Kopfes und 28 Schliffe (davon 18 aus der Schliffsammlung W. Gross, Berlin: Nr. 2571–2588).

Stratigraphie. Das Alter der Grey Hoek Schichten ist unsicher. Friend, F. 1961 und Winsnes, Th.S., Heintz, A. u. Heintz, N. 1966 (S. 21, 23) halten sowohl ein Alter von oberem Unterdevon als auch ein Alter von unterem Mitteldevon für möglich. Die bisher publizierte Fischfauna läßt eine genaue Einstufung nicht zu, die hier beschreibenen Palaeoniscoidea-Reste lassen einen Vergleich mit dem Baltikum zu, wo *Orvikuina*-Schuppen in der Luga-Stufe (Mitteldevon) auftreten. Ebenfalls für Mitteldevon sprechen die Pflanzenreste, allerdings sind beide Arten (*Arctophyton gracile* Schweitzer und *Psilodendrion spinulosum* Høeg) endemisch, nur aus den Grey Hoek Schichten bekannt. Auf Grund der Organisationshöhe der Pflanzen, vor allem von *Arctophyton gracile* Schweitzer, hält H. J. Schweitzer ein unterdevonisches Alter für ausgeschlossen, er stuft die Grey Hoek Schichten ins untere Mitteldevon (mittleres Eifelium) ein.

MORPHOLOGIE. Die Gattung *Orvikuina* wurde von W. Gross 1953 anhand eines kleinen Materials (20 Schuppen) aus dem Mittel Old Red des Baltikums aufgestellt. Ihm lagen nur langgestreckte Schuppen vor, diese Schuppen bilden auch den Hauptteil an dem Material aus Vaerdalen (453 Schuppen und Bruchstücke von Schuppen der Gestalt wie auf Abb. 14, 15 u. Taf. III, Fig. 2–6 dargestellt = 79% aller Schuppen). Mehr rhombische Schuppen sind seltener, Schuppen eines Aussehens wie auf Abb. 12 (= Taf. III, Fig. 1) 40 Exemplare (= 7%) und Schuppen mit isolierten, stark verzierten Rippen (Abb. 13 u. Taf. III, 7, 8) 77 Exemplare (= 13,5%). Wohl mag für das Vorherrschen der langgestreckten Schuppen sowohl im Baltikum als auch in Spitzbergen zum Teil selektive Ablagerung verantwortlich sein, aber da in Spitzbergen zusammen mit den langgestreckten Schuppen ebenfalls rhombische auftreten, ist anzunehmen, daß es sich bei *Orvikuina* um eine Palaeoniscoidea-Form mit vorwiegend langgestreckten Schuppen handelt. Die für die Ventralregion charakteristischen Schuppen müssen weit auf die Flanken hinaufreichen. Symmetrische Schuppen der ventralen oder der dorsalen Mittellinie sind äußerst selten (3 Exemplare = 0,5%).

Ein Merkmal der *Orvikuina*-Schuppen, das auch W. Gross 1953 hervorhebt (S. 101), ist das Fehlen einer Grube-Dorn-Gelenkung. Diese Gelenkung fehlt oft bei rhombischen Ganoidschuppen aus der Ventralregion. Bei *Orvikuina* ist aber auch an den rhombischen Schuppen der Flanken diese Gelenkung nicht vorhanden. Man sieht nur im hinteren Abschnitt des Dorsalrandes der rhombischen Schuppen (Abb. 13 u. Taf. III, Fig. 7, 8) eine Ausbuchtung nach dorsal, der eine seichte Vertiefung nahe dem Ventralrand auf der Innenseite entspricht. Eine Andeutung dieser Ausbuchtung am Dorsalrand zeigt in W. Gross 1953 die Abb. 8B (Taf. 6, Fig. 11). Auch ohne Dorn-Grube-Gelenkung überlagern sich die Schuppen stark, am Dorsalrand liegt ein breiter Knochensaum (" glatter Saum " bei W. Gross 1953, S. 101), der am Ventralrand der Innenseite in eine entsprechende Vertiefung hineingreift. Ein Kiel ist auf der Schuppeninnenseite trotz Fehlens der Dorn-Grube-Gelenkung ausgebildet, er tritt sogar manchmal bei den langgestreckten Schuppen schmal und stark hervor (Taf. III, Fig. 2b bzw. Gross, W. 1953, Abb. 8K).

Die vordere obere Ecke ist ausgezogen, ohne vom Vorder- oder Dorsalrand abgesetzt zu sein. Der Vorderrand ist gerade und nach caudal geneigt, manchmal ist er in einen oberen und einen unteren Abschnitt über eine schwache Ecke dazwischen geteilt (Abb. 12). Der Ventralrand verläuft gerade oder schwingt etwas nach ventral aus. Der Hinterrand endet meist in einer Spitze, seltener in zwei (31 Exemplare wie auf Abb. 12) oder sogar in drei (9 Exemplare), abgesehen natürlich von Schuppen des Aussehens wie Abb. 13.

Das freie Feld der langgestreckten Schuppen ist von einer einheitlichen Ganoinfläche bedeckt, die sich zum Vorderrand hin in einzelne Zungen auflöst. Die

Schuppen mit 2 oder 3 Zacken am Hinterrand besitzen ebenso viele durch tiefe Furchen voneinander getrennte Ganoinflächen, diese lösen sich ebenfalls nach vorne hin in Zungen auf und gelegentlich sind ihnen einzelne Flecken vorgelagert (Abb. 12a = Taf. III, Fig. 1), was auch bei manchen langgestreckten Schuppen zu beobachten ist (Abb. 15). Alle diese einheitlichen Ganoinflächen bauen sich aus zahlreichen Streifen auf, die sich jeweils dorsal und ventral an die Ganoinfläche anlagern—besonders deutlich in Abb. 15 (= Taf. III, Fig. 3)—und nach vorne in die einzelnen Zungen fortsetzen. An das Zentralfeld (1 in Abb. 15b) legt sich zuerst

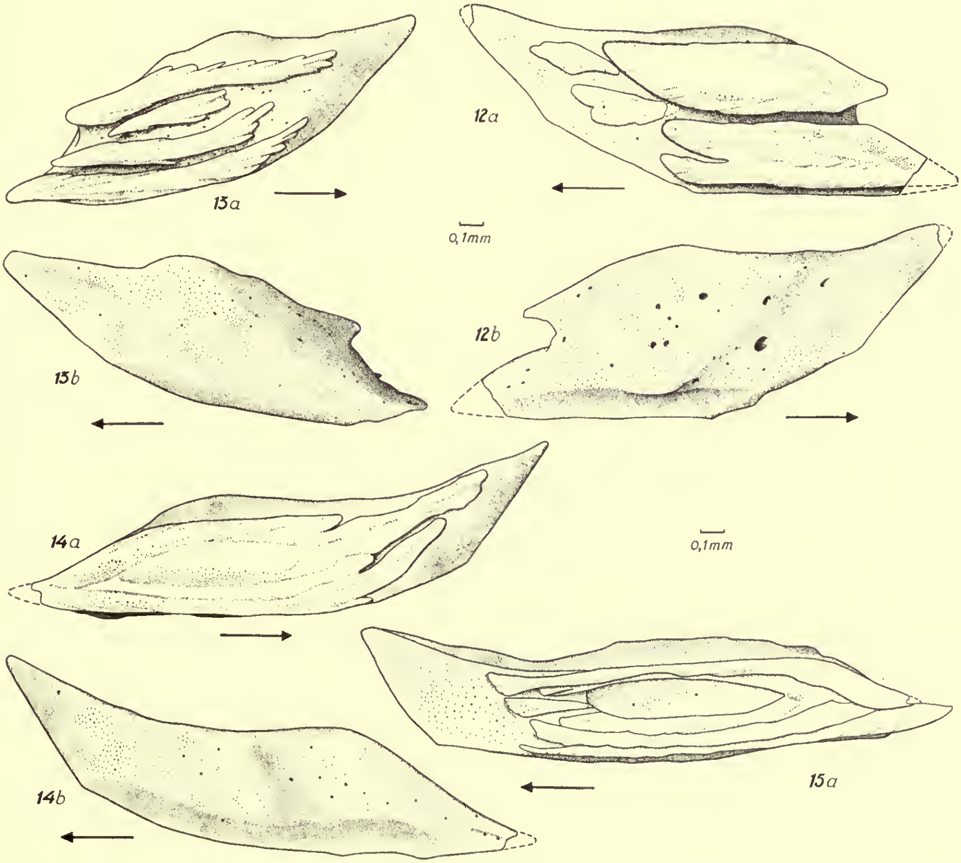


Abb. 12–15a. *Orvikuina* sp., Grey Hoek Schichten, unteres Mitteldevon, Westteil der Nordseite von V-Vaerdalen, Wood Bay, Spitzbergen. 12, Sto: P 6403. Schuppe der linken Körperseite vermutlich von der Körperflanke, Schuppe mit zwei flachen Ganoinrücken. a, Außenseite. b. Innenseite. × 32. 13. Sto: P 6408. Schuppe der rechten Körperseite aus der vorderen Körperhälfte, mit schmalen, stark verzierten Skulpturrippen. a, Außenseite. b, Innenseite. × 32. 14, Sto: P 6401. Schuppe der rechten Körperseite aus der Ventralregion, fast geschlossene Ganoindecke. a, Außenseite. b, Innenseite. × 32. 15a, Sto: P 6400. Schuppe der linken Körperseite aus der Ventralregion, fast geschlossene Ganoindecke, die die Wachstumsabfolge deutlich zeigt. Außenseite. × 32.

ventral ein Streifen an, der nächste folgt dorsal, dann wieder ventral und so weiter (Wachstumsabfolge 1–6 in Abb. 15b). Da man meist auf den Schuppen die einander entsprechenden ventralen und dorsalen Streifen vorfindet und da diese im caudalen Abschnitt der Schuppe, wo sie aneinander stoßen, eng aneinander liegen, ist zu folgern, daß beide Streifen in einer kurzen Zeitspanne nacheinander abgelagert werden (Gross, W. 1953, S. 105: " Zweizahl "). Abb. 16 zeigt diese Wachstumsabfolge im Schnitt. Auf das Ganoin des Zentralfeldes (1 in Abb. 15b) bzw. des vorher abgelagerten Streifens legt sich seitlich das Ganoin des nächsten Streifens. Das Dentin grenzt ohne Resorptionslinien aneinander. Die Ganoinfläche wird aber nicht nur nach dorsal und ventral sondern auch nach rostral vergrößert, und von rostral greifen die Streifen dann auf die ganze Ganoinfläche über (Abb. 18), so daß man das für *Orvikuina* typische Schnittbild mit übereinander liegenden Rippen erhält (Abb. 19).

Das Ganoin ist mit feinen Längsleistchen verziert. Diese treten besonders deutlich nahe dem Vorderrand hervor, sind aber auch am Ventral- und Dorsalrand der Ganoinstreifen ausgebildet (Abb. 12a, 14a) und heben innerhalb einer geschlossenen Ganoinfläche die Begrenzung der einzelnen Streifen hervor (Abb. 12a, 15a). Diese Skulptur der Längsleistchen tritt sehr kräftig auf den isolierten Rippen rhombischer Schuppen (Abb. 13a, Taf. III, Fig. 7a, 8) hervor. Diese rhombischen Schuppen zeigen die gleiche Wachstumsabfolge. Zuerst wird eine kurze Rippe im Zentrum angelegt, um die sich ventral und dorsal die nächsten Rippen allerdings getrennt von den vorhergehenden legen. Auch hier greifen später von rostral her Rippen über die früher angelegten hinweg (Taf. III, Fig. 9), so daß man das gleiche Schnittbild wie Abb. 19 erhält. Da alle Schuppen isoliert gefunden worden sind, ist es nicht ganz sicher, daß die rhombischen Schuppen mit den stark verzierten Rippen demselben Fisch angehören wie die langgestreckten Schuppen. Der histologisch gleiche Aufbau und die gleiche Schuppenform (Fehlen eines Dornes) sprechen aber sehr dafür, daß es sich hier um die stärker skulptierten Schuppen der vorderen Körperhälfte handelt. Und so ist anzunehmen, daß die Kopfknochen von *Orvikuina* sp. ebenfalls mit derartig stark skulptierten Rippen verziert sind. Fragmente, die Kopfknochen zuzuordnen sind, zeigen diese Skulptur, ebenso ein Fragment (PMO: A 34000) aus dem südlichen Teil Spitzbergens (Røykensåta, Stormbukta, Sörkapp Land: ebenfalls Grey Hoek Schichten).

Das Kanalsystem ist von Gross, W. 1953 (Abb. 11) im Ausschnitt dargestellt worden. Hier soll nur noch an einer Schuppe mit zwei Ganoinflächen der Zusammenhang zwischen zonarem Wachstum und Kanalsystem gezeigt werden (Abb. 17). Unter den beiden zentralen Ganoinflächen verläuft ein Längskanal, von dem zahlreiche Querkanäle abgehen und außerhalb der Ganoinüberdeckung ausmünden. Jedem neuen Streifen, der sich ventral oder dorsal an die zentrale Ganoinfläche anlagert, folgt ebenfalls ein Längskanal, der durch Querkanäle mit dem ersten Längskanal verbunden ist. Auf der Innenseite öffnen sich bei einigen Schuppen sehr große Poren der absteigenden Kanäle (Abb. 12b = Taf. III, Fig. 1b).

Histologie. Der histologische Aufbau der Schuppen (Abb. 16, 18, 19 u. Taf. IV, Fig. 4) stimmt mit dem von *Orvikuina vardiaensis* Gross (Gross, W. 1953, Abb. 9A, B) überein. Die Ausbildung von Ganoin- und Dentinschicht ist identisch.

Gelegentlich sieht man eine Schichtung im Ganoin. Das Ganoin der einzelnen Wachstumszonen überlagert sich randlich, ist stellenweise resorbiert besonders dort, wo es weit von Dentin überlagert wird (Abb. 19 Mitte). Die Dentinröhrchen gehen in alle Richtungen von den Kanälen ab und verzweigen sich nach dorsal gegen das Ganoin hin stark. Der Verlauf der Dentinröhrchen, die nach ventral gerichtet sind, ist unregelmäßiger. Im Bereich ventral der Kanäle sind keine Konturlinien zu beobachten wie im Dentin dorsal der Kanäle. Der ganze Bereich, der von Dentinröhrchen durchzogen wird, ist dunkelbraun gefärbt (Taf. IV, Fig. 4). Der Knochenschicht fehlen wie bei *Orv. vardiaensis* die Lakunen der Knochenzellen. Wegen der schlechten histologischen Erhaltung (häufig Umkristallisation) sind die Williamson'schen Kanäle meist nicht gut oder überhaupt nicht zu sehen. Der Längsschliff (Abb. 18) zeigt Williamson'sche Kanäle, die von oben (außen) in die Knochenschicht eindringen. Sie verlaufen gerade und verzweigen sich nur am Ende, sie sind also wie die Williamson'schen Kanäle in allen rhombischen Ganoidschuppen

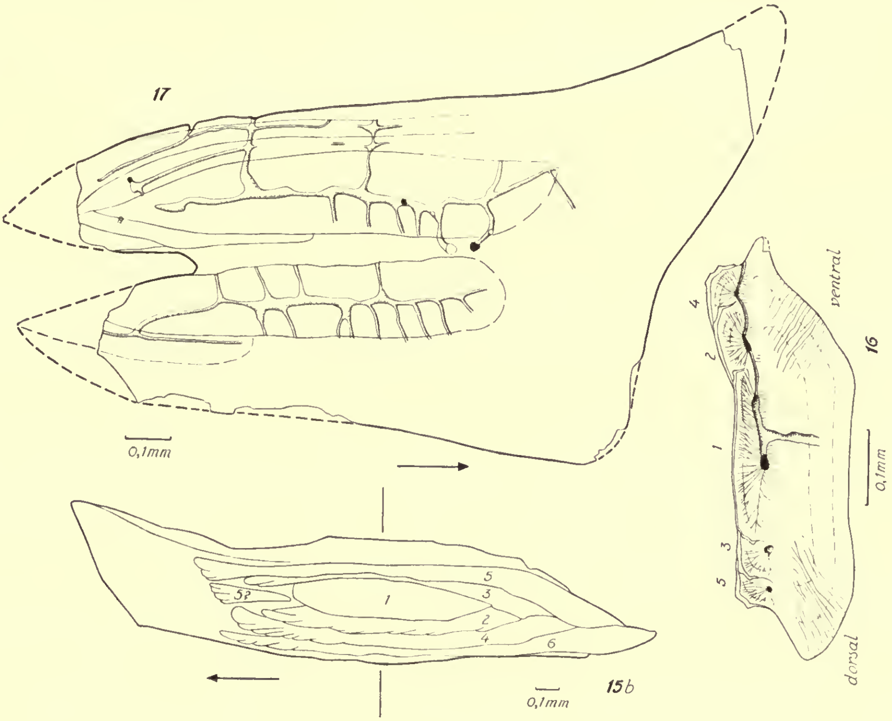
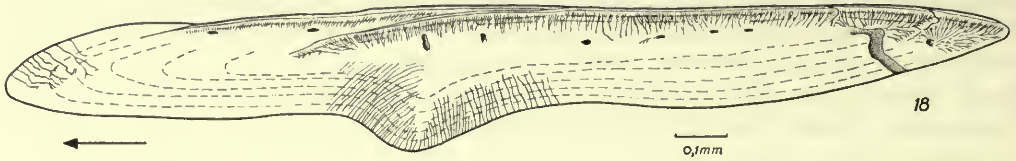


ABB. 15b, 16, 17. *Orvikuina* sp., Grey Hoek Schichten, unteres Mitteldevon, Westteil der Nordseite von V-Vaerdalen, Wood Bay, Spitzbergen. 15b, Sto: P 6400. Schuppe der linken Körperseite aus der Ventralregion, Schema der Wachstumsabfolge (1–6). × 32. 16, Gr.B.: 2579. Dorsal-ventraler Vertikalschliff mit Wachstumsabfolge 1–5. × 100. 17, Gr.B.: 2587. Horizontalschliff durch eine Schuppe der rechten Körperseite. Schuppe mit zwei flachen Ganoinrücken, dargestellt das Kanalsystem. × 60.

● = Öffnungen der Kanäle auf der Schuppenoberseite, ○ = Öffnungen der Kanäle auf der Schuppeninnenseite.



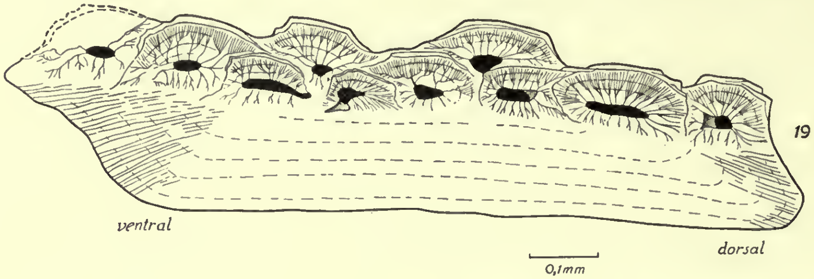


Abb. 18, 19. *Orvikuina* sp., Grey Hoek Schichten, unteres Mitteldevon, Westteil der Nordseite von V-Vaerdalen, Wood Bay, Spitzbergen. 18, Sto: S 2135. Rostral-caudaler Vertikalschliff. × 70. 19, Sto: S. 2137. Dorsal-ventraler Vertikalschliff. × 90.

geformt. Williamson'sche Kanäle, die von der Innenseite aufsteigen und unregelmäßig verlaufen, kann man nur in zwei Schliffen sehen (GrB: 2575 u. 2580). Aber auch hier ist die Erhaltung so schlecht, daß der genaue Verlauf nicht verfolgt werden kann. Der Unterschied zu den Sharpey'schen Fasern ist nur gering, sodaß man nicht feststellen kann, ob sie in den Bereich dieser übergehen oder nicht.

Vergleiche. Die hier beschriebenen Schuppen aus Spitzbergen stimmen in Form und Histologie sehr mit *Orv. vardiaensis* Gross aus dem Baltikum überein. Beide Formen besitzen langgestreckte Schuppen ohne Dorn, mit scheinbar einheitlicher Ganoinoberfläche und Längsleistchen an den Rändern des Ganoins. Die Anordnung und der Verlauf der Kanäle und der histologische Bau der Schuppen beider Fundpunkte stimmen völlig überein. Daß die Williamson'schen Kanäle im Material aus Spitzbergen selten zu sehen sind, liegt wohl nur an der schlechten histologischen Erhaltung dieses Materials.

Die Schuppen von *Orv. vardiaensis* unterscheiden sich nur dadurch von *Orvikuina* sp., daß die Ganoinoberfläche von caudal her stärker gegliedert und der Hinterrand mehrfach gezackt ist. Dieser Unterschied ist aber zu gering, um darauf eine neue Art zu begründen. Andererseits können die rhombischen Schuppen nicht zu einer Artdefinition herangezogen werden, da sie aus dem Baltikum nicht bekannt sind.

W. Gross 1953 (S. 109) vergleicht *Orvikuina* mit *Stegotrachelus*. Ein histologischer Vergleich beider Gattungen ist kaum möglich, da die Schuppen von *Stegotrachelus finlayi* Woodward u. White schwarz gefärbt sind und beim Schleifen nicht durchsichtig werden. Morphologisch unterscheiden sich die Schuppen beider Gattungen beträchtlich. So sind die Schuppen von *Stegotr. finlayi* an den Flanken höher als lang, langgestreckte Schuppen sind wenig vertreten, auch ist im Gegensatz zu *Orvikuina* eine Grube-Dorn-Gelenkung ausgebildet. Die Ganoinoberfläche ist meist geschlossen und an den Rändern mit sehr kräftigen Längsleistchen versehen, die weit auf die Ganoinoberfläche hinaufgreifen. Auffallend sind die großen Poren in der Ganoinoberfläche. In allen diesen Merkmalen gleichen die Schuppen von *Stegotr. finlayi* sehr den Schuppen von *Moythomasia nitida* Gross (Jessen, H. 1968, Abb. 4B).

Da *Orvikuina* die Dorn-Grube-Gelenkung fehlt, ist es nicht möglich, die Schuppen morphologisch mit Schuppen anderer Palaeoniscoidea zu vergleichen. Auf Grund des histologischen Baues steht *Orvikuina Dialipina* am nächsten (ausführlicher Vergleich siehe S. 356/357).

III. DISKUSSION ZUR HISTOLOGIE

Die Schuppen von *Ligulalepis*, *Dialipina* und *Orvikuina* besitzen ein gemeinsames Merkmal, bei allen ist das Dentin nur von einer dünnen Ganoinschicht überdeckt, besonders bei den unterdevonischen Gattungen *Ligulalepis* und *Dialipina*. Nahezu alle Palaeoniscoidea legen mehrere Ganoinschichten übereinander an (*Cheirolepis* im Mitteldevon bereits viele), nur bei einzelnen ist die Ganoinschicht dünn und einschichtig—außer den hier beschriebenen bei *Moythomasia laevigata* Gross (Gross, W. 1953, S. 100, Mitteldevon) und *?Gonatodus brainerdi* (Thomas) (Cavender, T. 1963, Taf. II, Fig. A, unteres Mississippian). Die dünne Ganoinschicht scheint ein ursprünglicher Charakter der palaeoniscoiden Ganoidschuppe zu sein.

Die Schuppen von *Dialipina* und *Orvikuina* besitzen keine Lakunen für Knochenzellen und bei beiden Gattungen treten unregelmäßige Williamson'sche Kanäle auf. Diese Ausbildung der Williamson'schen Kanäle wurde von T. Ørvig 1957*b* phylogenetisch ausgedeutet. Er sieht in den Abzweigungen der Williamson'schen Kanäle die Fortsätze von Knochenzellen, die sich nach einem ersten phylogenetischen Stadium der Konzentration um die Williamson'schen Kanäle in diese zurückgezogen haben sollen (Ørvig, T. 1957*b*, S. 487). Eine Konzentration von Knochenzellen um Kanäle ist vom rezenten *Polypterus* (Taf. IV, Fig. 2) und von drei triassischen Formen *Perleidus stochiensis* Stensiö (Stensiö, E. 1933, Taf. 39), *Scanilepis dubia* (Woodward) (Ørvig, T. 1957*b*, Abb. 2) und *Heterolepidotus* sp. (Schultze, H.-P. 1966, Abb. 47) bekannt. Nur bei *Perl. stochiensis* und *Heterolepidotus* sp. sind Knochenzellen zahlreich in der Nähe echter Williamson'scher Kanäle angeordnet. Bei *Scan. dubia* und *Polypterus* erfolgt die Konzentration der Knochenzellen um weite Kanäle, deren Lumen ein mehrfaches einer Knochenzelle beträgt. Diese Kanäle münden gelegentlich an der Oberfläche der Schuppe aus (Aldinger, H. 1937, Abb. 58), hierin entsprechen sie den " einfachen, weiten Kanälen " (Schultze, H.-P. 1966, Abb. 49) der lepidosteoiden Ganoidschuppe und wohl auch den Kanälen bei *Callichthys* (Ørvig, T. 1957b, Abb. 4B) und stehen in großem Gegensatz zu den Williamson'schen Kanälen, die nie die ganze Schuppe durchqueren. Bei den Kanälen von *Scanilepis* und *Polypterus* handelt es sich um aufsteigende Kanäle des Kanalsystems des Dentins und nicht um Williamson'sche Kanäle der Definition von T. Ørvig 1951, S. 365. So kann man die Konzentration der Knochenzellen bei *Polypterus* und *Scanilepis* wohl mit dem Zustand bei *Callichthys* vergleichen nicht aber mit den Williamson'schen Kanälen bei den devonischen Gattungen; vielleicht läßt sich auch eine Entwicklung von einem Zustand ähnlich wie bei *Polypterus* und *Scanilepis* zu einem Zustand wie bei *Callichthys* begründen.

Die weiten Kanäle bei *Scanilepis* und *Polypterus* zeigen noch einige Gemeinsamkeiten, die echten Williamson'schen Kanälen fehlen. In dem Bereich, wo der Kanal von Knochenzellen umgeben wird, trennt ihn von den Knochenzellen ein Bereich konzentrischer Lamellen mit einer feinen radialen Streifung (Taf. IV, Fig. 3). Dieser Bereich wird nahe der Dentinschicht von vielen unregelmäßigen Kanälchen durchzogen (vermutlich Dentinröhrchen, siehe Ørvig, T. 1957*b*, Fig. 1); ähnliche, aber noch unregelmäßigere Kanälchen gehen sowohl bei *Scanilepis* als auch *Polypterus* (Sewertzoff, A. N. 1932, Taf. 7, Fig. 10) von den weiten Kanälen aus, die annähernd horizontal am Schuppenrand ausmünden. Die Schuppen von *Scanilepis* und *Polypterus* zeigen also im histologischen Bau große Ähnlichkeiten was H. Aldinger 1937 (S. 227/228) bereits hervorhob.

Im Gegensatz zu den Kanälen bei *Polypterus* und *Scanilepis* entsprechen die Kanäle in den Schuppen von *Dialipina* und *Orvikuina* ganz der Definition nichtvasculärer Williamson'scher Kanäle (Ørvig, T. 1951, S. 365). Ihr Lumen ist viel geringer als das einer Knochenzelle, was bereits W. Gross 1953 betont (S. 104 oben). Sie sind daher wohl auch wie alle nichtvasculären Williamson'sche Kanäle im Sinne Ørvig's als die Ausläufer einer sich odontoblastenähnlich zurückziehenden Knochenzelle zu deuten. Ihr wechselndes Lumen (An- und Abschwellen) findet sich auch bei Williamson'schen Kanälen anderer Schuppen (Schultze, H.-P. 1966, Abb. 55b), nur verzweigt sich der Fortsatz der basal der Schuppe sitzenden Zelle bei diesen beiden devonischen Gattungen viel stärker als gewöhnlich. Diese Abzweigungen sind aber nicht als Fortsätze mehrerer Knochenzellen zu deuten, die in den Williamson'schen Kanälen sitzen, da das Lumen der Kanäle zu eng für Knochenzellen ist. Den weiten Kanälen in den Schuppen von *Scanilepis* und *Polypterus*, um die sich Knochenzellen konzentrieren, entsprechen in den Schuppen von *Dialipina* und *Orvikuina* (Abb. 16, 18 u. Gross, W. 1953, Abb. 9B) die Kanäle, die vom Kanalsystem zur Schuppenbasis absteigen und in deren Nähe sich wie in der gesamten Knochenschicht keine Knochenzellen finden.

So ist T. Ørvig 1957*b* (S. 487) wohl beizupflichten, daß Knochengewebe ohne Knochenzellen bei den Actinopterygiern zumindest zweimal unabhängig voneinander bei den Palaeoniscoidea und den Teleostei auftritt. Aber ein Sichzurückziehen der Knochenzellen in irgendwelche Kanäle während der Phylogenie ist abzulehnen.[1] Mit der Bildung des Knochengewebes müssen immer Knochenzellen in Verbindung stehen. Daß die Lakunen nicht in der Knochenschicht erhalten bleiben, kann zweierlei Ursachen haben: entweder werden die Lakunen während der Bildung der Knochenschicht wieder ausgefüllt (Moss, M. L. 1961) oder sie werden während des ganzen Bildungsprozesses nicht eingeschlossen, bleiben immer am Rand der Knochenschicht liegen. So sind auch in den Schuppen von *Polypterus*, *Scan. dubia*, *Perl. stochiensis* und *Heterolepidotus* sp. die Knochenzellen im übrigen mehr oder weniger gleichmäßig auf die gesamte Knochenschicht verteilt.

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[1] J. D. Currey 1961 vergleicht die Kanaldichte in der Knochenbasis von *Scanilepis* (etwa 37 Kanäle pro mm.^{2}) und *Orvikuina* (etwa 2300 Kanäle pro mm.^{2}) und die Kanäle selbst (*Scanilepis* mit vasculären und *Orvikuina* mit nichtvasculären Kanälen). Er kommt zu der gleichen Schlußfolgerung, d.h. er lehnt ebenfalls eine Entwicklung azellulären Knochens in Sinne Ørvig's ab: "Though *Orvikuina* is seen, therefore, to be highly specialized, it shows a different kind of specialization from that shown by *Scanilepis*, and it has not simply travelled further along the line of specialization started by *Scanilepis* " (Currey 1961, S. 190).

Nach Einreichung des Manuskripts zum Druck machte mich Prof. Dr. W. Gross freundlicherweise noch auf diese Arbeit aufmerksam.

IV. STRATIGRAPHIE UND FAUNA

Die Sedimente der drei Lokalitäten, wo die hier beschriebenen Palaeoniscoidea vorkommen, entstammen marinem Milieu; zusammen mit den Vertebratenresten treten Invertebraten und Conodonten auf. Die Vertebratenfauna mit *Ligulalepis* vom Murrumbidgee River (Australien) ist mit Korallen, Trilobiten, Brachiopoden, Gastropoden, Scaphopoden, Cephalopoden und Conodonten (Browne, I. 1959) vergesellschaftet, also eindeutig als marin gekennzeichnet. Im Vergleich dazu ist die Invertebratenfauna, die zusammen mit *Dialipina* und *Orvikuina* sp. gefunden worden ist, spärlicher. Mit *Dialipina* (NW-Kanada) zusammen finden sich Ostracoden, Conchostraken (*Estheria*- und *Leaia*-ähnliche), Brachiopoden (*Lingula*) und Conodonten, mit *Orvikuina* sp. (Spitzbergen) zusammen Ostracoden und Lamellibranchiaten. Beide Sedimente enthalten aber auch Pflanzenreste (z.B. *Trochiliscus* sowohl in den kanadischen als auch in den Grey Hoek Schichten) und so mögen beide Sedimente als küstennahe Bildungen angesehen werden, wie es P. F. Friend 1961 (S. 103) für die Grey Hoek Schichten annimmt.

Besonders auffällig an dem Vertebratenmaterial aus den Grey Hoek Schichten ist die Vergesellschaftung der Palaeoniscoidea mit Thelodontierschuppen und zwar den trompetenförmigen, wie sie T. Ørvig 1957*c* (Abb 2, 3) aus dem südlichen Teil Spitzbergens beschrieben hat. Auch in den Essigsäurelösungen des Gesteins dieser Lokalität (Røykensåta, Stormbukta, Sörkapp Land, Südspitzbergen) fand sich ein Palaeoniscoidea-Rest (PMO: A 34000). Die trompetenförmigen Thelodontierschuppen treten auch zusammen mit dem Holotyp von *Homostius arcticus* Heintz (Heintz, A. 1933, Taf. 9, Fig. 1) auf, sind aber außerhalb Spitzbergens unbekannt.

Eine weitere Faunenkomponente der Grey Hoek Schichten sind *Porolepis*-ähnliche Schuppen, die E. Jarvik 1950 (Abb. 32B) und T. Ørvig 1957*a* (Abb. 8C) abgebildet haben. Schuppen mit denselben charakteristischen Merkmalen sind auch von anderen Lokalitäten in Spitzbergen, z.B. Jacobsdalen (Ørvig, T. 1957*a*, Abb. 8A, B), und aus dem Polnischen Mittelgebirge bekannt (Kulczycki, J. 1961, Taf. 6, Fig. 1–8). Der Quarzit, in dem die *Porolepis*-ähnlichen Schuppen im südlichen Teil des Polnischen Mittelgebirges auftreten, wird ins Emsium eingestuft. Der gleiche Schuppentyp ist ebenfalls mit *Dialipina* vergesellschaftet. Sofern die stratigraphische Einstufung der Sedimente der drei Lokalitäten zutrifft—sie ist für alle drei Ablagerungen unsicher—müßte man eine stratigraphisch weite Verbreitung dieser *Porolepis*-ähnlichen Schuppen vom Unterdevon bis ins Mitteldevon annehmen.

Gemeinsam haben die Faunen von Spitzbergen und Australien Arthrodiren und Acanthodier, beide Faunenkomponenten fehlen im kanadischen Material, treten aber zusammen mit *Orvikuina vardiaensis* im Baltikum auf. Dagegen sind aus den Grey Hoek Schichten in Spitzbergen keine Dipnoer bekannt, die sowohl in den australischen (Hills, E. S. 1958), den kanadischen (Jarvik, E. 1967) als auch den baltischen Ablagerungen (Gross, W. 1942) auftreten.

Die Vertebratenfauna vom Murrumbidgee River (Australien) ist reichhaltiger als die der beiden anderen Fundpunkte, so findet man in den Rückständen der Essigsäurepräparation Reste von *Onychodus*, *Ohiolepis* und *Ohioaspis*, Formen, die in Schichten aus dem Unter-Mitteldevon Grenzbereich der verschiedensten Fundpunkte auftreten: Bonebeds in Ohio, Indiana and Kentucky (Wells, J. W. 1944, oberstes Unterdevon und unterstes Mitteldevon), Onondaga Kalk von Clifton Springs, New York (oberstes Unterdevon mit *Ohioaspis*),[1] Heisdorfer Schichten bei Wetteldorf im Rheinischen Schiefergebirge (oberstes Unterdevon mit *Ohiolepis*)[1]. Aus diesem Vergleich heraus erscheint auch die Einstufung der Schichten am Murrumbidgee River ins oberste Unterdevon durch die Vertebratenfauna bestätigt.

V. SUMMARY

Palaeoniscoid scales are described from Lower Devonian rocks of Southeastern Australia and Northwestern Canada, and from Middle Devonian rocks of Spitsbergen. The scales from Spitsbergen (the Grey Hoek beds, probably Middle Devonian) are very similar in shape and histological structure to the scales of *Orvikuina vardiaensis* Gross from the Middle Devonian of the Baltic region. The composition of the undivided surface of the ganoin is demonstrated and the growth of single stripes of dentine + ganoin is shown. Because 79 % of the scales are elongated, it is supposed that elongated scales of the ventral region extended far up on the flanks in *Orvikuina*. The peg on the dorsal border of the scales is absent.

New genera and species are erected for the scales from Lower Devonian rocks of Northwestern Canada and Southeastern Australia, because the scales show characters unknown in scales of other palaeoniscoid species. *Dialipina salgueiroensis* n.g. n. sp. from Northwestern Canada has scales with separate ridges of dentine + ganoin. The ridges end near the caudal border of the scales and the new dentine + ganoin complex is deposited as isolated spots occupying positions between the ridges and also between the spots in front of them.

Ligulalepis toombsi n.g. n. sp. from New South Wales, Australia, has deep scales with a prominent antero-dorsal process. On the inner surface of the scales two ridges are present. The first ridge near the rostral border of the scale is identical with the ridge on rhombic scales which is penetrated by Sharpey's fibres. On the caudal border of the second " ridge " the canal system of the dentine ends, and the canals open caudally. In rostro-caudal section the scales show a shape comparable only with a rostro-caudal section of a *Cheirolepis* scale, but the differences in morphology and histology between them render improbable a close phylogenetic relationship between *Ligulalepis* and *Cheirolepis*.

The scales of *Orvikuina*, *Dialipina* and *Ligulalepis* have thin, single-layered ganoin, which is apparently a primitive character of palaeoniscoid scales. Cells are absent

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[1] Material im Besitz von Dr. T. Ørvig, Naturhistoriska Riksmuseet, Paleozoologiska sektionen, Stockholm.

in the bone of the scales of *Dialipina* and *Orvikuina*, but irregular canals of Williamson are present in both forms. These are non-vascular canals of Williamson (according to the definition of T. Ørvig 1951, p. 365), each with an odontoblast-like cell in the end on the inner surface of the scale. The processes given off along the canals probably cannot be interpreted as processes of bone cells placed in the canals, because the canal lumen is much smaller than the volume of lacunae containing bone cells. If this is so, the concentration of bone cells around canals in the scales of *Scanilepis* probably cannot be interpreted as a stage in the evolution of acellular bone tissue like that of *Dialipina* and *Orvikuina* (cf. Ørvig, T. 1957*b*, p. 487). Rather, the canals with the concentration of bone cells in *Scanilepis* would seem to belong to the canal system of the dentine, being ascending canals from the inner surface of the scales. Similar canals are present in the scales of *Orvikuina* and *Dialipina*, and in these forms they are clearly distinguishable from canals of Williamson. The canals in the scales of *Scanilepis* are in other ways much like the canals in the scales of the recent *Polypterus* (Aldinger, H. 1937, p. 227/228) and there is the same concentration of bone cells around the canals.

The scales of *Dialipina salgueiroensis*, *Ligulalepis toombsi* and *Orvikuina* sp. were found in marine beds. Together with *Orvikuina* sp., occur horn-like thelodontid scales (known only from the Devonian of Spitsbergen) and *Porolepis*-like scales. The *Porolepis*-like scales are associated also with the scales of *Dialipina salgueiroensis*. Together with *Ligulalepis toombsi* occur fragmentary remains of other vertebrates (*Ohiolepis*, *Ohioaspis*, *Onychodus* etc.). The fauna as a whole is comparable with the " micro-vertebrates " of other localities from the upper Lower Devonian.

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TAF. 1

FIGS. 1–8. *Ligulalepis toombsi* n.g. n.sp., Unterdevon, New South Wales, Australien.

FIG. 1. BM: P. 48853. *Spirifer yassensis* Kalk, " right bank of Murrumbidgee, boulders probably nearly *in situ*, on shore and up hillside, 2500 yds. due E. of Majurgong T.S. " Hohe Schuppe aus der Region dicht hinter dem Schultergürtel, rechte Körperseite. a. Außenseite. b. Innenseite. × 20.

FIG. 2. BM: P 48851. *Spirifer yassensis* Kalk, Lokalität wie P. 48853 (= Fig. 1). Hohe Schuppe mit Grübchenorgan aus der dorsalen Region dicht hinter dem Schultergürtel, linke Körperseite. a. Außenseite. b. Innenseite. × 20.

FIG. 3. BM: P 48857. *Spirifer yassensis* Kalk, " left bank of Murrumbidgee, boulders on shore and hillside above, 1300 yds at 29° magnetic from Majurgong T.S. " Bruchstück einer hohen Schuppe der rechten Körperseite aus der vorderen Körperhälfte, Außenseite. × 20.

FIG. 4. BM: P 48864. Holotyp. *Spirifer yassensis* Kalk (unterer Teil), Lokalität wie P 48853 (= Fig. 1). Hohe Schuppe aus der vorderen Körperhälfte der linken Körperseite. a. Außenseite. b. Innenseite. × 20.

FIG. 5. BM: P 48854. ?*Spirifer yassensis* Kalk, " left bank of Murrumbidgee, base of steep low cliff 1300 yds at 27° magnetic from Majurgong T.S. " Schuppe der rechten Körperseite aus der vorderen Körperhälfte, Außenseite. × 20.

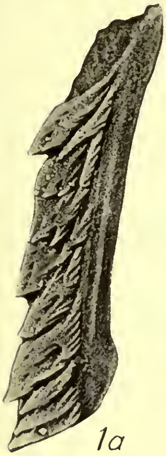
FIG. 6. BM: P 48858. *Spirifer yassensis* Kalk, Lokalität wie P 48857 (= Fig. 3). Schuppe der rechten Körperseite wohl aus der Körpermitte. a. Außenseite. b. Innenseite. × 20.

FIG. 7. BM: P 48860. *Spirifer yassensis* Kalk (nahe der Basis), " left bank of Murrumbidgee, rock face in gully 1200 yds at 39° magnetic from Majurgong T.S. " Bruchstück einer hohen Schuppe, Blick auf die Hinterkante des zweiten " Kiels " mit Öffnungen des Kanalsystems (= ö), links Innenseite, rechts Außenseite der Schuppe. × 20.

FIG. 8. BM: P 48849. Bloomfield Kalk, " not *in situ*, on hillside south of inlet, 2750 yds at 4° magnetic from Majurgong T.S. " Seitenlinienschuppe der linken Körperseite aus der hinteren Körperhälfte. a. Außenseite. b. Innenseite. × 20.

FIG. 9. *Dialipina salgueiroensis* n.g. n. sp., Unterdevon, ?Delorme Formation, Anderson River, gerade stromaufwärts des Zusammenflusses mit dem Ross River (68° 11′ Nord/125° 49′ West), Nordwestkanada. NMC 11617. Schuppe der linken Körperseite aus der vorderen Körperhälfte, Außenseite. × 20.

FIG. 10. *Cheirolepis canadensis* (Whiteaves), Oberdevon, Scaumenac Bay, Kanada, Sto: S 927. Rostral-caudaler Vertikalschnitt ungefähr parallel zur Seitenlinie. × 100.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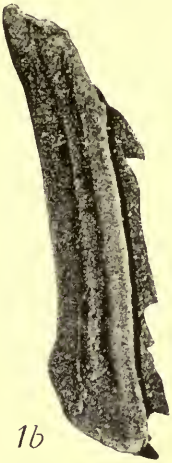
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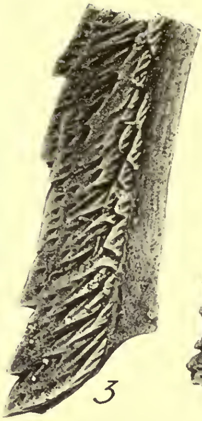
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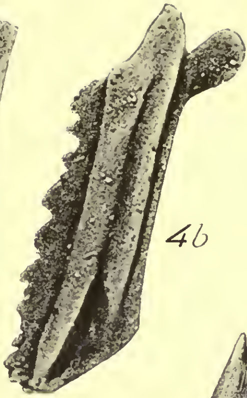
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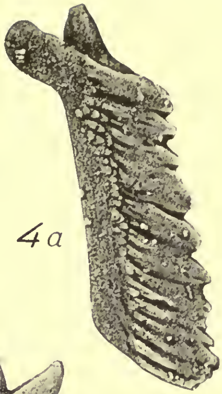
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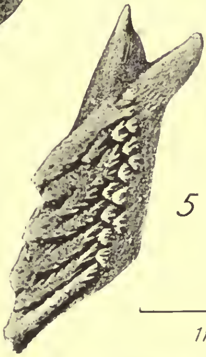
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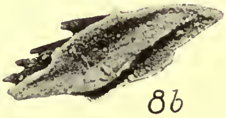
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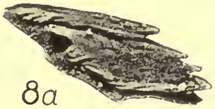
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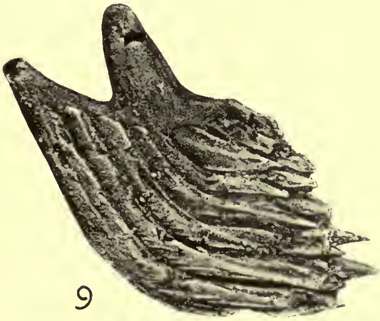
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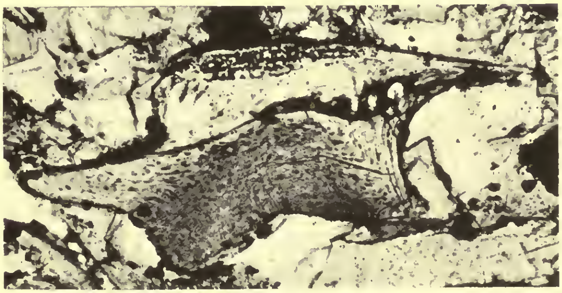
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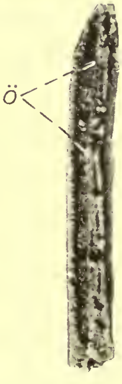

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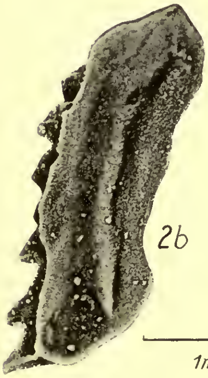
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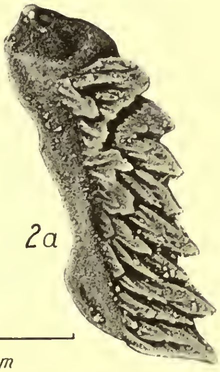
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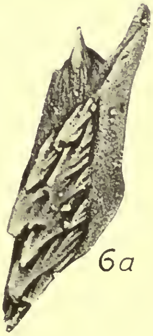
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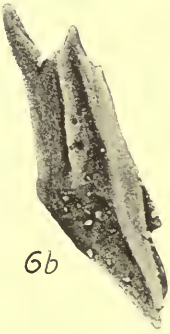
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TAF. 2

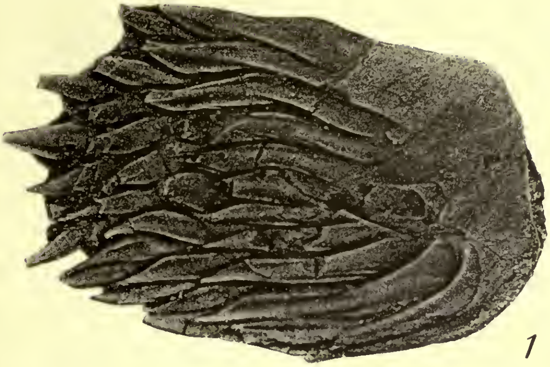
Figs. 1–4. *Dialipina salgueiroensis* n.g. n. sp., Unterdevon, ?Delorme Formation, Anderson River, gerade stromaufwärts des Zusammenflusses mit dem Ross River (68° 11′ Nord/125° 49′ West), Nordwestkanada.

Fig. 1. NMC 11609, Schuppe der rechten Körperseite, vermutlich eine Analschuppe, Außenseite. ×20.

Fig. 2. NMC 11608, Holotyp. Schuppe der linken Körperseite aus der vorderen Körperhälfte. a. Außenseite. b. Innenseite. ×20.

Fig. 3. NMC 11611. Schuppe der rechten Körperseite, vermutlich aus der Körpermitte (= Abb. 11), Außenseite. ×20.

Fig. 4. NMC 11616, Teil des Schultergürtels (?Cleithrum). a. Außenseite. b. Innenseite. ×15.



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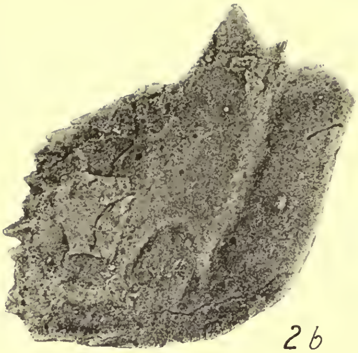

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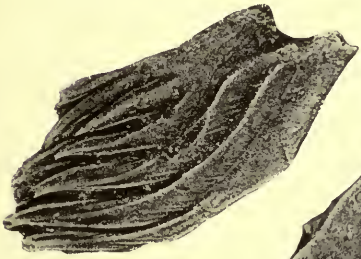

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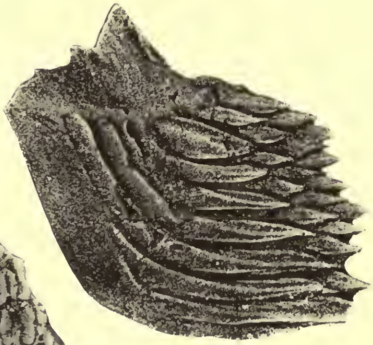

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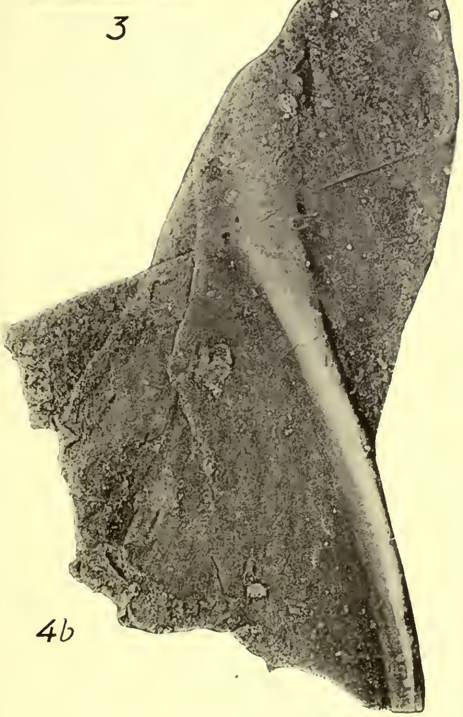

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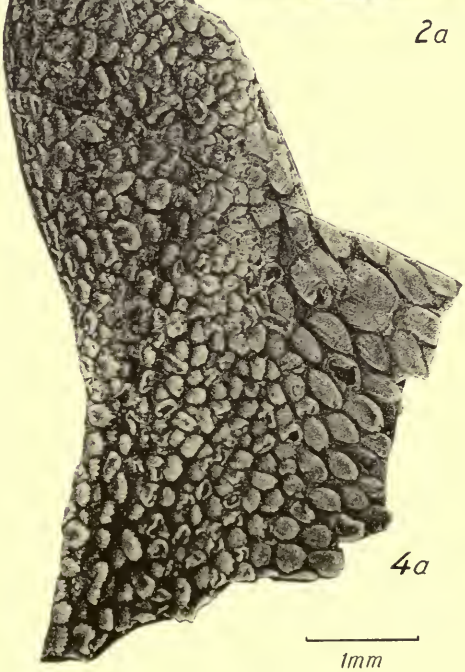

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TAF. 3

FIGS. 1–9. *Orvikuina* sp., Grey Hoek Schichten, unteres Mitteldevon, Westteil der Nordseite von V-Vaerdalen, Wood Bay, Spitzbergen.

FIG. 1. Sto: P 6403. Schuppe der linken Körperseite vermutlich von der Körperflanke. a Außenseite. b. Innenseite. × 27.

FIGS. 2–6. Schuppen aus der Ventralregion.

FIG. 2. Sto: P 6406. Schuppe der linken Körperseite. a. Außenseite. b. Innenseite. × 27.

FIG. 3. Sto: P. 6400. Schuppe der linken Körperseite, Außenseite. × 27.

FIG. 4. Sto: P 6401. Schuppe der rechten Körperseite. a. Außenseite. b. Innenseite. × 27.

FIG. 5. Sto: P 6405. Schuppe der linken Körperseite. Außenseite. × 27.

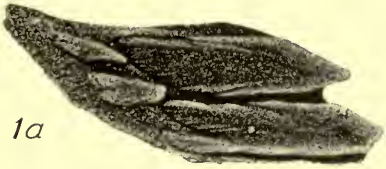
FIG. 6. Sto: P 6402. Schuppe der linken Körperseite. Außenseite. × 27.

FIGS. 7, 8. Schuppen der rechten Körperseite aus der vorderen Körperhälfte mit schmalen, stark verzierten Skulpturrippen.

FIG. 7. Sto: P 6408. a. Außenseite. b. Innenseite. × 27.

FIG. 8. Sto: P 6414. Außenseite. × 27.

FIG. 9. Sto: P 6407. Großschuppe der linken Körperseite mit schmalen, stark verzierten Skulpturrippen. Außenseite. × 27.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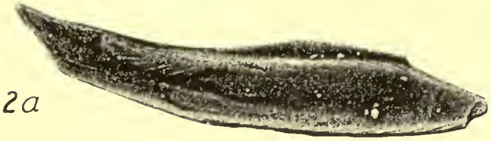
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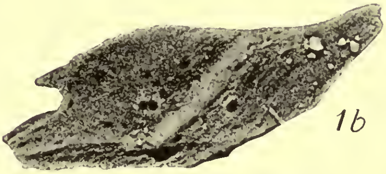
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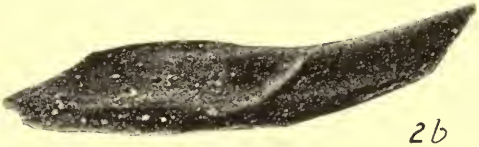
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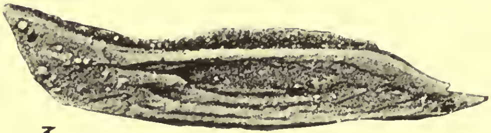
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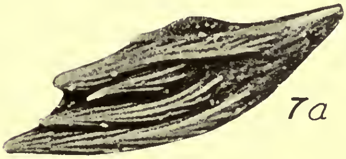
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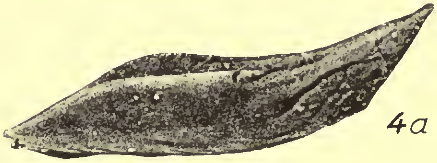
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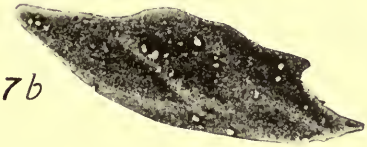
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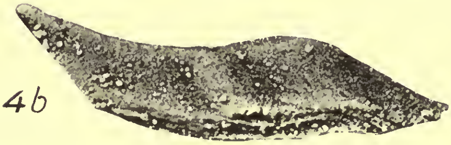
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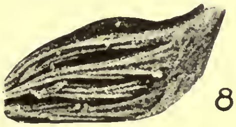
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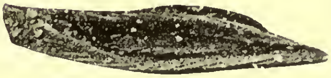
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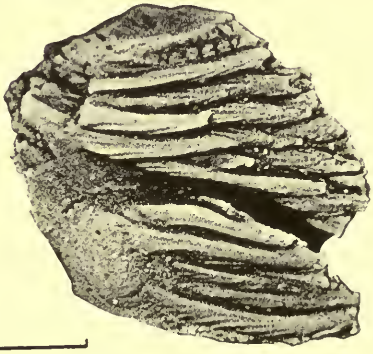
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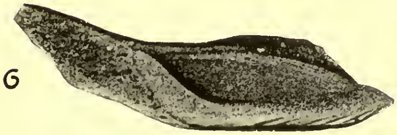
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TAF. 4

FIG. 1. *Ligulalepis toombsi* n.g. n. sp., *Spirifer yassensis* Kalk, Unterdevon, " top of spur falling west to left bank of Murrumbidgee, 1800 yds at 347° magnetic from Majurgong T.S. " New South Wales, Australien. BM: P 48855. Hohe Schuppe der rechten Körperseite etwa aus der Körpermitte, Durchlichtaufnahme in Wasser. ×45.

FIG. 2. *Polypterus bichir* Geoffr. BM: P 48829 (Schliff von E. S. Goodrich), Vertikalschliff, Ausschnitt aus der Knochenschicht. ×150.

FIG. 3. *Scanilepis dubia* (Woodward), Rhät, Bjuv, Skåne, Südschweden. Sto: S 1212. Horizontalschliff, Ausschnitt, Knochenzellen um Williamson'schen Kanal. ×200.

FIG. 4. *Orvikuina* sp., Grey Hoek Schichten, unteres Mitteldevon, Westteil der Nordseite von V-Vaerdalen, Wood Bay, Spitzbergen. Sto: S 2137. Dorsal-ventraler Vertikalschliff. ×75.

FIGS. 5–7. *Dialipina salgueiroensis* n.g. n. sp., Unterdevon, ?Delorme Formation, Anderson River, gerade stromaufwärts des Zusammenflusses mit dem Ross River (68° 11′ Nord/125° 49′ West), Nordwestkanada.

FIG. 5. NMC 11605. Dorsal-ventraler Vertikalschliff durch den Kiel. ×75.

FIG. 6. NMC 11607. Rostral-caudaler Vertilakschliff. ×75.

FIG. 7. NMC 11604. Rostral-caudaler Vertikalschliff. ×75.

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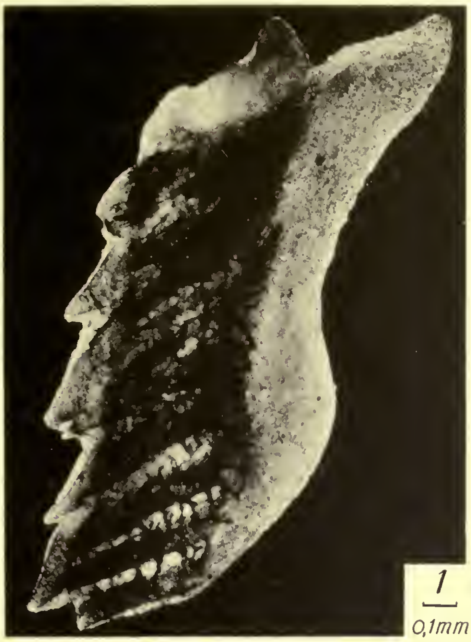
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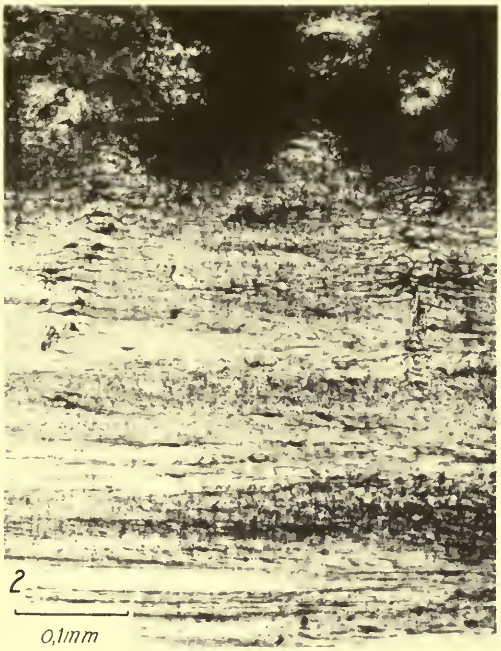
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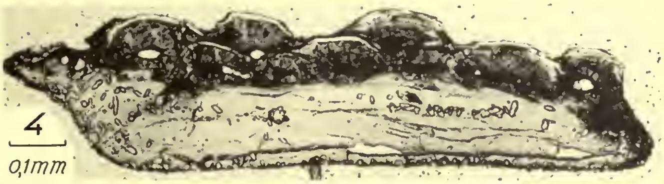
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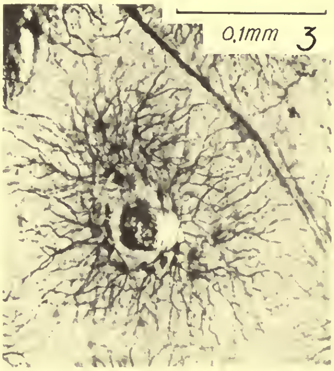
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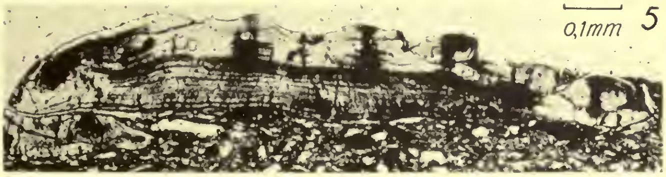
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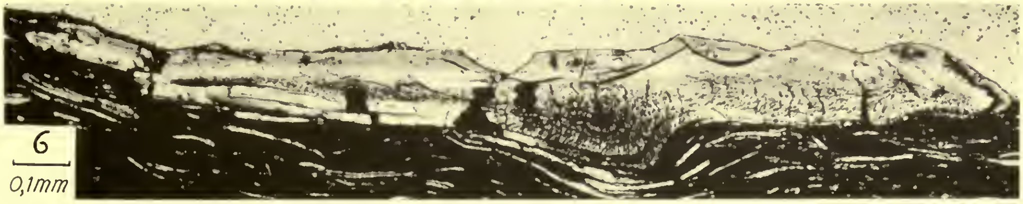
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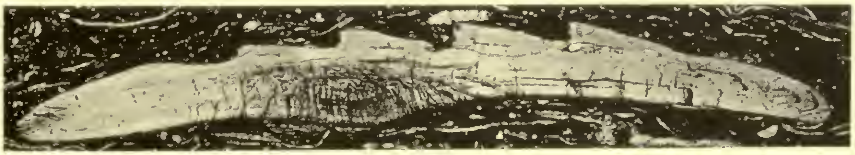
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